Tree Physiology 8, 23–36

Winter desiccation and injury of subalpine red spruce

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Received April 3, 1990

Summary

Montane red spruce (*Picea rubens* Sarg.) in the northeastern United States has undergone a decline during the past two decades. One symptom associated with the decline syndrome is the episodic browning of first-year foliage in early spring. To examine the potential role of winter desiccation in this browning, the water relations of red spruce foliage in a subalpine forest on Mt. Moosilauke, New Hampshire, USA, were monitored from January to May, 1989. All sampled trees lost water during the winter and the first-year foliage on some trees turned brown in early spring. The relative water content of first-year shoots during the winter was a significant predictor of spring browning; red spruce trees that showed browning had desiccated faster and reached lower relative water contents. Damaged trees also had more closely packed needles and lower cuticular resistances to water loss. The first-year shoots had a significantly lower average relative water content than older shoots before and after browning. Cuticular resistance to water loss decreased with elevation. Sun-exposed shoots lost more water than shaded shoots because of solar heating of needles. Winter desiccation can occur before the decline-related spring browning of red spruce foliage.

Introduction

The phenomenon of winter desiccation—the development of winter water deficits in evergreen foliage—has been observed in several montane coniferous tree species. Cuticular transpiration, coupled with frozen soil or conducting tissue, is thought to be the primary cause (Sakai 1968, Tranquillini 1979). The two major factors influencing cuticular transpiration are needle microclimate and cuticular resistance to water vapor transfer (Gates 1968, Marchand 1972, Tranquillini 1976). Solar heating of needles above air temperature may be the most important microclimatic factor (Marchand 1972, Baig and Tranquillini 1980). For conifer needles, which have a high resistance to water loss, wind may play an insignificant role (Baig and Tranquillini 1980) or even reduce transpiration through needle cooling (Marchand 1972). At high elevations, the cuticular resistance to water loss is lower, possibly because of inadequate cuticle development during the shorter growing season (Baig and Tranquillini 1976, 1980, Sowell et al. 1982, DeLucia and Berlyn 1984, Cochrane and Slatyer 1988). Injury to needles at high elevations has been attributed to severe winter desiccation, and has been used as an explanation for the maintenance of alpine treeline (Sakai 1970, Tranquillini 1976, 1979, Sowell et al. 1982, Hadley and Smith 1983, DeLucia and Berlyn 1984). Winter injury is not always associated with

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desiccation, however, and it is likely that in some regions other processes also play a role (Slatyer 1976).

Red spruce (*Picea rubens* Sarg.) is a shade-tolerant conifer with an approximate maximum age of 350 years. It exists at low elevations in southeastern Canada and the extreme northeastern United States and at high elevations in the Appalachian and Adirondack mountain ranges of the eastern United States. In the northern Appalachians, red spruce exists from about 700 to 1200 m above mean sea level and timberline occurs at about 1400 m above mean sea level. The other major species in these subalpine forests are balsam fir (*Abies balsamea* (L.) Mill.) and paper birch (*Betula papyrifera* var. *cordifolia* Marsh (Regel)) (Siccama 1974).

Since the mid-1960s, the growth rates and basal areas of red spruce in the northern Appalachians and Adirondacks have been declining (Siccama et al. 1982, Scott et al. 1984, Hornbeck and Smith 1985). Visible symptoms associated with decline include browning of the youngest needles in late winter or early spring (Friedland et al. 1984). These symptoms have been attributed to winter injury (Friedland et al. 1984) and events appear to be sporadic (Johnson et al. 1986). Both freezing injury and desiccation injury have been considered as possible causes.

Kincaid and Lyons (1981) found no significant change in the water potential of red spruce shoots on Mt. Monadnock, New Hampshire, USA, over four weeks during the winter of 1978 or over two weeks during the following autumn. They suggested that winter desiccation never occurs in red spruce on Mt. Monadnock. However, rates of cuticular transpiration are highly dependent on microclimate, the depth of soil freezing, and the cuticular development of the previous year's foliage. These factors may change dramatically from year to year and thus one year's investigation may not be adequate to disprove the occurrence of winter desiccation (Tranquillini 1979).

The primary purpose of this study was to monitor the water status of red spruce shoots on a limited number of trees during the winter of 1989 on Mt. Moosilauke, New Hampshire, USA. If desiccation occurred, a secondary objective was to look for possible relationships between the degree of desiccation and any observed browning. We also wished to determine the influences of needle microclimate, cuticular resistance, and shoot morphology on red spruce winter water status and on injury if it occurred.

Methods

Study sites and sampling

Mt. Moosilauke (44°01′ N, 70°51′ W, 1465 m elevation) is one of the westernmost peaks of the White Mountains of north-central New Hampshire in the northern Appalachian Mountains. Vegetation grades from northern hardwood forests at low elevations through coniferous subalpine forests at higher elevations to alpine tundra near the summit (Reiners and Lang 1979).

Temporal study Four sites on the mountain within the subalpine zone were established to study temporal changes in the water content of first-year (1988) shoots of red spruce. The sites were located on the east and west sides of the mountain and at two elevations, 840 and 990 m above mean sea level. At each site the same red spruce trees were sampled 11 times from January 13 to May 6, 1989 (three, four, or five trees per site; total $n = 16$). On each sampling date two different branches with a total of at least five whole 1988 shoots were cut from each tree at about 5 m above ground level. The samples were immediately sealed in plastic bags, frozen in a dark, insulated box filled with snow, and transported to the laboratory.

Elevational study Six sites were established on the west side of the mountain at 760, 840, 910, 990, 1070, and 1140 m above mean sea level to study elevational patterns. Four trees at each site were sampled on March 10, 1989 by the methods described for the temporal study.

Foliar age study One tree on the east side at 880 m above mean sea level, one tree on the west side at 880 m, and one tree on the east side at 990 m were sampled on February 11, February 24, and March 17, respectively, to study the influence of needle age on relative water content. Needles on internodes formed in 1988 and in the three previous years were examined.

Microclimate study One site for studying needle microclimate was established on a ridge to the east of Mt. Moosilauke at 950 m and shoots were sampled from four trees at this site on March 7, 1989.

Laboratory measurements

On arrival at the laboratory, the degree of browning of the sampled foliage was visually assessed. The number of shoots with more than 25% of their needles brown on the last two sampling dates (April 15 and May 6, n = 10 shoots) was used to determine a damage rating (from 0 to 10) for each tree.

Relative water content The procedure of Marchand and Chabot (1978) was followed to determine the relative water content (RWC) of recut shoots. The shoots were weighed, then floated on deionized, distilled water in covered petri dishes for 24 h at approximately 3 °C in the dark. The samples were then blotted dry, reweighed, and oven-dried at 70 °C for at least three days before weighing again. Relative water content was computed from the equation:

$$\mathrm{RWC} = (w_\mathrm{f} - w_\mathrm{d})/(w_\mathrm{t} - w_\mathrm{d}) \times 100, \qquad (1)$$

where RWC is the relative water content in %, and w_f, w_d, and w_t are the fresh, oven-dried, and fully hydrated (turgid) weights, respectively (Turner 1981). The water content of hydrated tissue as a percentage of oven-dry weight (WC) was also recorded. A total of 848 shoots were analyzed for the temporal study, 120 for the elevational study, 76 for the foliar age study, and 60 for the microclimate study.

Morphology After oven-drying the shoots for RWC determinations, needles were removed from the stems. The bare stems were then weighed and their length and number of lateral buds recorded (n = 1104 stems). The number of needles on 471 shoots was counted and the lengths of ten randomly selected needles from each of 260 shoots were measured. To determine total shoot surface area geometrically, an estimate of needle perimeter was needed. A preliminary estimate of needle width, based on measurements of 34 needles with an ocular micrometer, was about 0.9 mm (0.95 mm ± 0.10 SD). The estimated needle width was multiplied by a red spruce perimeter/width ratio of 2.7 (R. Boyce, personal communication) to give an estimated perimeter of 2.4 mm. The estimated needle perimeter, the average needle length, and the number of needles were used to compute geometrically the total shoot surface area for shoots used in the cuticular resistance determinations ($n = 260$). The total shoot dry weight and bare stem dry weight were used to compute needle dry weight as a percentage of total shoot dry weight ($n = 1104$). The number of needles and the stem length were used to compute needle packing (needles per mm stem, $n = 471$). The total needle dry weight was divided by the number of needles to obtain the average individual needle weight ($n = 471$). All of the morphology measurements were made after oven-drying. Thus, because some shrinkage probably occurred, the reported values are underestimates of the true values. However, because only the relative size is important in comparisons among groups, the conclusions were not affected by this underestimation.

Cuticular transpiration and resistance After hydration for RWC determination, samples from the elevational study ($n = 120$), from the microclimate study ($n = 60$), and from March 17 of the temporal study ($n = 80$) were placed in a dark chamber at 3 °C and 20% relative humidity. The samples were weighed at approximately 24-h intervals for 3 to 4 days and then oven-dried as in the RWC determination. Water loss in the first 24-h period was disregarded as possible stomatal transpiration and subsequent water loss down to an RWC of 40% (WC of 60%) was used to calculate the cuticular transpiration rate in g m^{-2} ks^{-1}. This range corresponds to the 60 to 90% WC range used by Hadley and Smith (1983) to measure the cuticular transpiration of Engelmann spruce (*Picea engelmanii* Parry). In addition, a preliminary analysis revealed that at an RWC below 40%, low water potential affects the transpiration rate of red spruce needles. Cuticular transpiration was used to calculate cuticular resistance according to the equation:

$$R_c = (C_l - C_a)/T, \tag{2}$$

where R_c is the water vapor diffusion resistance (primarily cuticular) in ks m^{-1}, C_l and C_a are the leaf and air water vapor densities in g m^{-3}, and T is the transpiration rate in g m^{-2} ks^{-1} (Kramer 1983). In calculating water vapor densities, we assumed that needle and chamber were isothermal and that within-needle air space was saturated.

Climate and needle microclimate

At each of the four sites established to study temporal changes, CR-10 dataloggers (Campbell Scientific) measured soil water every hour with gypsum conductivity blocks at a depth of 30 cm, and recorded averages of the readings every 6 h throughout the study.

At the site established to study microclimate, another datalogger recorded relative humidity, ambient temperature, and the temperatures of both sun-exposed and shaded first-year needles every 2 min and recorded averages of the readings every 20 min, from February 19 to March 7, 1989. A shielded, combined RH sensor-thermistor probe measured relative humidity and ambient temperature. Needle temperatures were measured by wrapping fine-wire, copper-constantan thermocouples around needles (Hadley and Smith 1983).

Statistical analyses

To assess the influence of elevation and aspect on the various observations, a two-way nested analysis of variance was performed with a type III test of hypotheses using trees (nested within elevation and aspect) as an error term. To determine how well various measurements predicted which trees would become brown at the end of the winter, and because *a posteriori* classification of data violates the assumptions of analysis of variance, a frequency-weighted stepwise discriminant analysis was used (Sokal and Rohlf 1981). The variables included in the stepwise analysis for each sampling date included RWC, needle packing, cuticular resistance, shoot length, total shoot dry weight, individual needle weight, needle length, and the elevation and aspect of the sites. The observations used in the analysis were the average values for each tree ($n = 16$).

Results and discussion

Desiccation

The average relative water content (RWC) of first-year shoots decreased significantly from 88.6% (0.3 SE) on January 13 to 69.4% (1.3) on March 24 and then increased to 84.3% (0.8) by May 6 (Figure 1a). The average water content as a percentage of oven-dry weight (WC) was 133.3% (0.9) on January 13, 96.5% (2.9) on March 24, and 110.2% (3.0) on May 6. Field RWC was significantly related to field WC by the equation: RWC = 0.358 (0.008 SE) × WC + 39.28 ($R^2 = 0.710$, $P < 0.0001$). Other investigators have reported water contents of wintering conifers similar to the average values observed at the beginning and end of this study (Marchand and Chabot 1978, Baig and Tranquillini 1980, Kincaid and Lyons 1981). However, in contrast to the results of other researchers, neither elevation nor aspect had a significant ($P < 0.05$) effect on the relative water content in the temporal study. Soil water became available in late March (data not shown), at about the same time the average water content increased (Figure 1a). This recharge is consistent with predictions based on experimental desiccation and soil thawing (Havis 1965).

Others have observed similar desiccation in wintering montane conifers near treeline (Sakai 1970, Hansen and Klikoff 1972, Tranquillini 1976, Baig and Tranquillini 1980, Hadley and Smith 1986). Models of winter cuticular transpiration

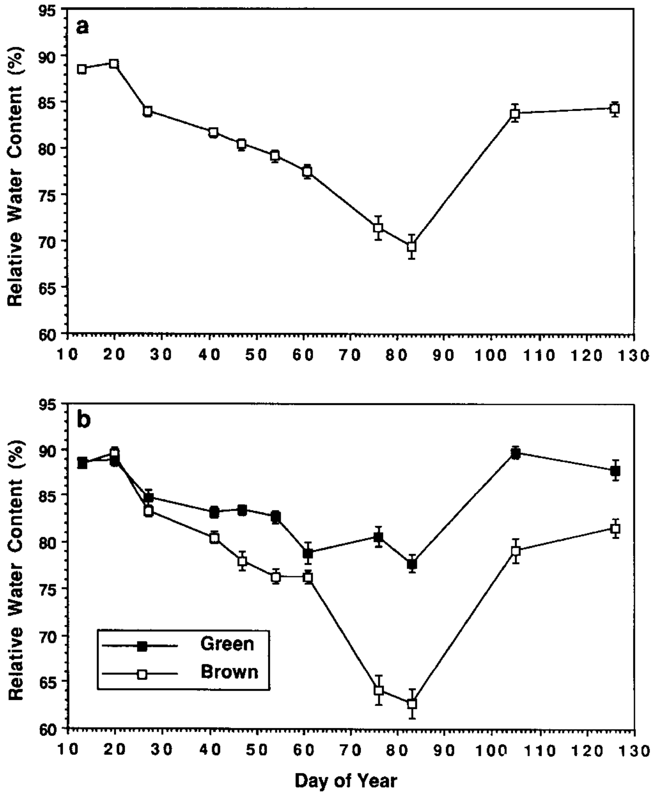

Figure 1. Variation in the relative water content of red spruce 1988 shoots on Mt. Moosilauke, New Hampshire, during the winter of 1989. (a) Average relative water content of all samples ($n = 80$) with standard errors indicated by bars. (b) Average relative water contents of shoots on trees that showed visible damage in early spring (brown, damage rating > 7) and those that appeared healthy (green, damage rating < 4). See Table 1 for damage ratings of individual trees.

also predict significant desiccation (Sowell et al. 1982). Several studies of winter water relations in which winter desiccation in conifers was observed were conducted during winters of low snowfall. Low, early snow cover causes earlier and deeper soil freezing which may result in a longer period of water unavailability and less chance of water recharge to foliage on warm days (Sakai 1968, Hansen and Klikoff 1972, Tranquillini 1982). There was very low snow cover during December of 1988 and January of 1989 in New Hampshire.

Tranquillini (1979) reported that winter desiccation does not occur in closed-canopy forests. He suggested that winter desiccation is the controlling factor in alpine treeline maintenance. The present results indicate that desiccation is not confined to the upper elevational limits of red spruce and can occur even in closed stands at middle elevations.

Visible injury and its relation to desiccation

No appreciable needle discoloration was observed before March. Mild yellow discoloration was observed on some first-year shoots in early and mid-March. These shoots became deep orange-brown by late March and early April. The injury appeared identical to the decline-related damage observed by Friedland et al. (1984) in the Green Mountains of Vermont. Of the sixteen trees sampled in the temporal study, the first-year shoots of nine became brown (Table 1).

By February 10, the average RWC of the trees was a significant ($P = 0.0023$, $R^2 = 0.59$) predictor of early spring injury (Table 2). With the exception of one sampling date, relative water content continued to be a significant ($P < 0.05$) predictor of early spring damage (Table 2). Ultimately, the trees that were to show injury desiccated faster and reached lower minimum water contents (Figure 1b). On March 24, the average RWC of damaged trees was 62.8% (1.5), whereas that of undamaged trees was 77.8% (0.9) (Table 1). In spring, the water content of damaged trees did not fully return to values measured at the beginning of the winter (Figure 1b). Gas embolisms (which have been observed in high elevation red spruce tracheids, M. Tyree, personal

Table 1. Damage rating and the average minimum water content, cuticular resistance, and needle packing by tree of 1988 shoots of red spruce on Mt. Moosilauke, New Hampshire during the winter of 1989. Numbers in parentheses are standard errors of the means.

Side	Elevation (m)	Damage rating[1]	Minimum RWC (%)[2,3]	Minimum WC (%)[2,3]	Needle packing (needles mm^{-1})	Cuticular resistance (ks m^{-1})
East	990	10	48.2 (2.7)	39.9 (1.7)*	2.20 (0.06)	–[4]
West	990	10	55.9 (7.4)	67.2 (16.5)	2.80 (0.04)	62 (3)
West	840	10	64.6 (3.9)*	80.5 (10.8)*	2.09 (0.06)	73 (3)
West	990	10	64.5 (1.6)	79.7 (5.7)	1.89 (0.05)	67 (8)
East	840	8	56.3 (1.2)	81.7 (4.4)	2.21 (0.05)	65 (3)
East	840	8	57.4 (0.4)*	78.9 (2.2)*	2.26 (0.06)	65 (4)
West	840	8	66.0 (2.6)	90.8 (4.8)	1.89 (0.04)	90 (9)
East	990	8	69.6 (2.7)*	102.8 (5.7)*	2.32 (0.05)	66 (6)
West	990	8	72.4 (2.5)*	97.1 (5.7)*	2.09 (0.05)	80 (4)
West	990	3	77.9 (3.0)	104.7 (3.2)	2.30 (0.06)	91 (14)
West	840	3	78.8 (1.0)	117.7 (0.5)	2.00 (0.04)	117 (7)
East	990	2	68.0 (1.5)	89.6 (4.7)	1.77 (0.05)	87 (6)
East	840	0	72.9 (1.4)*	100.5 (2.1)*	2.04 (0.05)	51 (5)
East	840	0	78.4 (1.7)	113.8 (2.6)	1.77 (0.07)	61 (7)
East	840	0	79.0 (1.5)*	107.0 (3.1)*	1.59 (0.05)	96 (5)
West	840	0	84.3 (0.2)	136.3 (1.2)	1.62 (0.04)	91 (5)
Average (standard error) of:						
Damaged (rating > 7)			61.7 (1.5)	79.8 (3.8)	2.20 (0.03)	71 (2)
Undamaged (rating < 4)			89.9 (0.9)	128.3 (2.5)	1.87 (0.03)	85 (4)

[1] Number of sampled shoots (out of 10) with more than 25% foliage brown on April 15 and May 6.

[2] RWC = relative water content. WC = water content as a percentage of oven-dry weight.

[3] Those trees which reached minimum water contents on March 17 are indicated by asterisks. All other trees reached minimum water contents on March 24. Values are averages of the water contents of five shoots per tree.

[4] Foliage on this tree was visibly injured at the time of the cuticular resistance determination and adequate measurements could not be made.

Table 2. Results of a frequency-weighted, stepwise discriminant analysis used to determine how well measurements obtained during the winter of 1989 on Mt. Moosilauke, New Hampshire explained the condition of red spruce foliage the following spring.

Day of year	Relative water content		Other significant predictors			Total model	
	R^2	P-value	Variable	R^2	P-value	R^2	P-value
13		ns	Needle packing	0.367	0.028	0.367	0.028
20		ns	Needle packing	0.350	0.026	0.350	0.026
27		ns	Needle packing	0.369	0.016	0.369	0.016
41	0.586	0.002	Elevation	0.477	0.009	0.690	0.008
			Cuticular resistance	0.349	0.034		
			Aspect	0.271	0.068		
47	0.283	0.041	Needle packing	0.241	0.063	0.504	0.011
54	0.625	0.001	Elevation	0.300	0.034	0.652	0.001
61		ns	Needle packing	0.308	0.026	0.308	0.026
76	0.700	<0.001	Aspect	0.308	0.032	0.705	<0.001
83	0.537	0.001	None			0.537	0.001
105	0.532	0.002	Cuticular resistance	0.233	0.068	0.592	0.002
126	0.566	0.002	Cuticular resistance	0.452	0.008	0.654	0.004
			Aspect	0.264	0.060		

Note: For individual predicting variables, the R^2 value is the squared partial correlation. For the total multivariate model, the R^2 value is the average squared canonical correlation computed from Pillai's trace. For individual predicting variables, the P-value is computed from an F-statistic from a one-way ANOCOVA. For the total multivariate model, it is computed from an F-approximation to Wilks' lambda, the likelihood ratio statistic.

communication) or permanent injury may have made it impossible for damaged needles to become fully recharged with water (Larcher and Siegwolf 1985).

Although winter injury is not always associated with desiccation (Slatyer 1976), it appears that desiccation played some role in the winter injury observed in the present study. If desiccation is the direct cause of the observed browning, it appears that the critical RWC is about 70% (Table 1), which would correspond to a WC of about 85%. Hadley and Smith (1983) report that, at a WC below 90%, winter-exposed Engelmann spruce needle viability declines. Tranquillini (1979) reported critical winter WCs between 60 and 90% in stone pine (*Pinus cembra* L.) and Norway spruce (*Picea abies* (L.) Karst).

Visible browning did not necessarily happen at the same time as cell injury so desiccation was not necessarily the cause of the browning. Water loss may have been a secondary result of some other type of injury that occurred in the winter but whose effects were not visible until early spring. Wardle (1981) showed that needles of Engelmann spruce sampled in the summer can be made more prone to desiccation and injury by artificial freezing. Freezing injury may occur in first-year red spruce foliage in early January at temperatures as high as −34 °C (DeHayes et al. 1990). Rapid needle temperature fluctuations, or other winter processes that might induce cell injury, could also initiate desiccation (White and Weiser 1964, Wardle 1981, J. Hadley, personal communication).

The first-year shoots of many red spruce trees on Mt. Moosilauke other than those sampled turned brown in early spring. We also observed browning in other areas of the Green Mountains of Vermont, the Adirondack Mountains of New York, and the White Mountains of New Hampshire during spring 1989. This was the first time such widespread spring browning had been observed since 1984.

The influence of needle morphology and cuticular resistance

The results of the shoot morphology and cuticular resistance analyses are presented in Table 3. Needle packing significantly ($P < 0.05$) predicted spring injury on four sampling dates (Table 2) with damaged trees having more closely packed needles. The needle packing of trees that showed early spring browning averaged 2.20 (0.03) needles mm^{-1}, whereas that of visibly healthy trees averaged 1.87 (0.03) needles mm^{-1} (Table 1). Greater needle packing increases the aerodynamic resistance to heat transfer and results in greater needle to air temperature differences (Smith and Carter 1988). The air boundary layer resistance to water vapor transfer is negligible compared to winter cuticular resistance so, in winter, high needle temperatures will increase transpiration through a dominant effect on the needle to air water vapor density difference. If winter water loss was responsible for early spring injury, then microclimate effects could explain the relationship between needle packing and browning.

Cuticular resistance was also a significant ($P < 0.05$) predictor of browning on three sampling dates (Table 2) with damaged trees having lower cuticular resistances than undamaged trees. The cuticular resistance of injured trees averaged 71 (2) ks m^{-1}, whereas that of visibly healthy trees averaged 85 (4) ks m^{-1} (Table 1). Low cuticular resistance may have increased transpiration resulting in greater water loss. However, the measurements were made on only one sampling date in late winter close to the time of visible injury.

There were no significant effects of elevation or aspect on shoot morphology or cuticular resistance of trees in the temporal study, although in the more extensive elevational study we found lower cuticular resistance at higher elevations (Figure 2).

Elevational patterns

Cuticular resistance decreased with elevation (Figure 2, cf. Baig and Tranquillini

Table 3. Shoot morphologies and cuticular resistances of 1988 shoots of red spruce on Mt. Moosilauke, New Hampshire during the winter of 1989.

Variable	Average	Standard error	n
Oven-dry weight of shoots (g)	0.147	0.003	844
Shoot length (mm)	36.1	0.4	844
Needle packing (needles mm^{-1})	2.05	0.02	240
Needle length (mm)	9.73	0.04	800
Needle weight (mg)	1.53	0.02	240
Cuticular resistance (ks m^{-1})	77	3	73

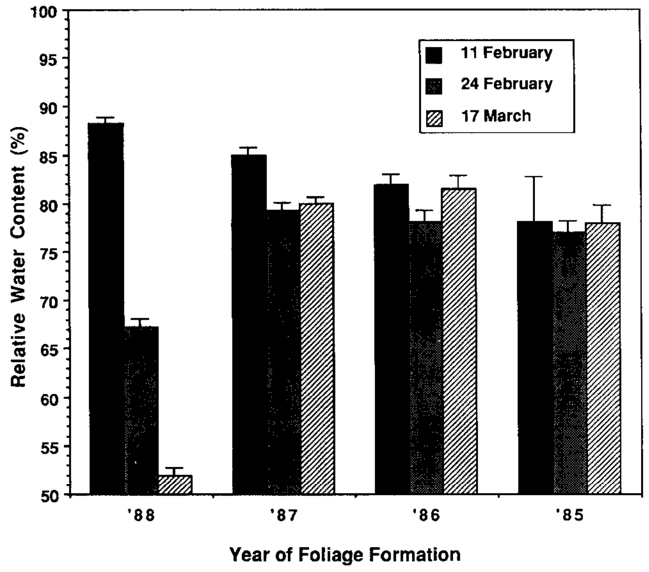

Figure 2. Decrease with elevation of cuticular resistance of red spruce 1988 foliage sampled on March 10, 1989 on Mt. Moosilauke, New Hampshire. Average cuticular resistance of 20 samples at each elevation are shown with standard errors indicated by bars. Cuticular transpiration, gravimetrically measured at 3 °C and 20% relative humidity, was used to calculate cuticular resistance.

1980, Sowell et al. 1982, DeLucia and Berlyn 1984). This phenomenon has been attributed to shorter and cooler growing seasons at higher elevations resulting in less cuticle development (Baig and Tranquillini 1976, Sowell et al. 1982, DeLucia and Berlyn 1984). Winter cuticular resistances for other conifers range from 46 to 400 ks m^{-1} and average around 200 ks m^{-1} within a forest (Sowell et al. 1982). In the present study, the average cuticular resistance of trees at 1140 m was 50 (2) ks m^{-1}, whereas that of trees at 760 m was 92 (3) ks m^{-1} (Figure 2). Thus, it appears that the cuticular resistances measured in the present study were within, but at the low end, of the reported range.

Patterns related to shoot age

On February 24, before browning was observed, the youngest (1988) shoots were significantly drier than older shoots (Figure 3). On March 17, after some browning was observed, the 1988 shoots were extremely desiccated (Figure 3). The 1988 shoots were also the only shoots showing visible injury. These results are consistent with, but do not confirm, the hypothesis that desiccation is the cause of the observed browning. DeHayes et al. (1990) found that first-year foliage is also the most susceptible to freezing injury.

One criticism of the theory that desiccation is responsible for winter injury is the lack of uniform early spring browning among shoots within the same branches and among needles within the same shoots even though water should be evenly redistributed during winter thaws (Wardle 1981). The present results indicate that such water

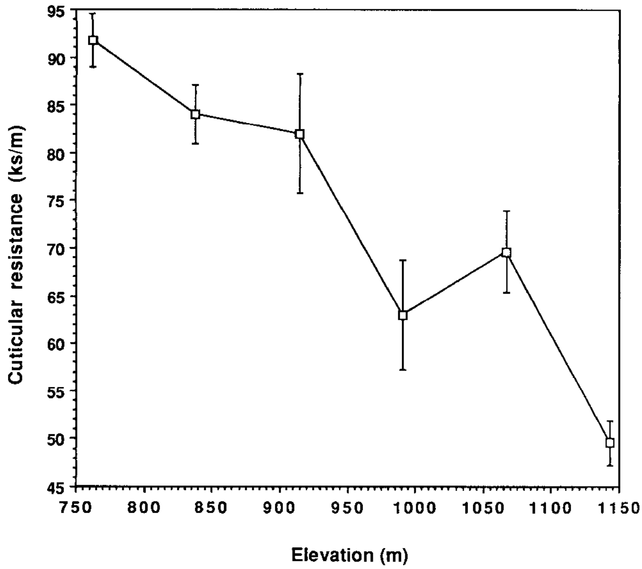

Figure 3. The relative water content of red spruce shoots of four different age classes on Mt. Moosilauke, New Hampshire during the winter of 1989. Average relative water contents and standard errors (indicated by bars) are shown for three different trees, sampled on three separate dates.

redistribution does not occur. Gas bubbles in the xylem, which can be produced in winter by freezing (Zimmerman and Brown 1971), could block water redistribution among different age shoots. Thus, if first-year foliage transpires more rapidly than older foliage, significant water deficits would develop in, and be confined to, first-year shoots, as was observed in the present study (Figure 3). Gas embolisms could also delay spring recharge (Larcher and Siegwolf 1985).

The influence of microclimate on transpiration

The average RWC of shaded shoots near the center of the trees was 71.8% (0.8) on March 7, whereas the average RWC of more sun-exposed shoots at the top and outside of the trees was 69.0% (0.6), a significant ($P = 0.013$) difference. There was no significant difference in the cuticular resistance between the two groups of shoots (date not shown), although there was a difference in microclimate (Figure 4).

The midday temperatures of red spruce needles averaged about 1 °C warmer than ambient temperatures with a maximum average difference of about 4 °C. Midday temperatures of sun-exposed needles (at the top of the crown and tips of the branches) were higher than those of shaded needles (within the crown) (cf. Tranquillini 1979, Hadley and Smith 1987). Such heating is predicted by models of conifer needle energetics (Tibbals et al. 1964).

The midday needle to air water vapor density difference in this study, which was computed from needle temperatures, ambient temperatures, and ambient relative humidities, was highest in sun-exposed needles (Figure 4). As predicted by theory

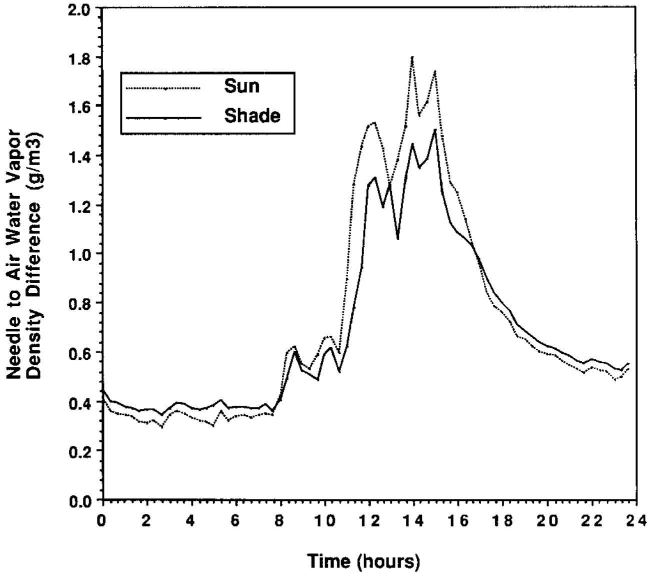

Figure 4. Diurnal variation in the needle to air water vapor density difference of sun-exposed and shaded red spruce needles on Mt. Moosilauke, New Hampshire from February 19 to March 7, 1989 at 950 m above mean sea level. The water vapor density difference was computed from needle temperature, ambient temperature, and relative humidity data taken every 2 minutes, averaged over 20 minutes.

(e.g., Gates 1968, Marchand 1972) and shown by Pisek and Tranquillini (1951), this temperature-induced increase in the needle to air water vapor density difference increases the transpiration rate. Sowell et al. (1982) predicted that a 1 °C increase in midday whitebark pine needle temperature would result in a 9% increase in the total water transpired during a winter and a 5 °C increase would result in a 48% increase in total water transpired.

Sun-exposed foliage desiccates more than shaded foliage. Hadley et al. (1990) observed that sun-exposed foliage also tends to show more spring browning than shaded foliage. Friedland et al. (1984) observed browning of foliage at the tops of crowns and tips of branches on many red spruce after the winter of 1984. Patterns in desiccation are again consistent with patterns in injury.

Conclusions

The water relations of red spruce foliage in a subalpine forest on Mt. Moosilauke, New Hampshire, were monitored from January to May 1989. First-year shoots desiccated during the winter and some turned brown the following spring. Winter relative water content was a significant predictor of spring browning; red spruce trees that showed browning had desiccated faster and reached lower relative water contents. Needle packing and cuticular resistance were also significant predictors of spring browning with damaged trees having more closely packed needles and lower cuticular resistances to water vapor transfer than undamaged trees.

Patterns in water loss were consistent with patterns in injury. First-year shoots were more desiccated than older shoots on the last two of three sampling dates, cuticular resistance decreased with elevation, and sun-exposed shoots were more prone to water loss than shaded shoots because of solar heating of needles.

These results are consistent with, but do not confirm, the hypothesis that winter desiccation causes the observed spring browning of red spruce foliage. Preliminary data indicate that desiccation is not occurring during the winter of 1990.

Acknowledgments

We thank D. Payne and D. Kistner for extensive and skilled help in the field. J. Hadley made valuable contributions to the study and wrote numerous and helpful comments on an earlier version of this manuscript. A. Boulanger, H. Caloto, D. Girard, R. Miotke, and P. Resor helped with field work under sometimes extreme conditions. S. Russo-Savage and J. Hornig assisted with field operations and provided equipment. G. Berlyn, R. Boyce, D. DeHayes, G. Hawley, and D. Wang provided valuable review. G. McHugo provided valuable statistical advice. This project was funded in part by the Andrew W. Mellon Foundation, New York, NY, the Rockefeller Center, Dartmouth College, Hanover, NH and the USDA Forest Service Spruce-Fir Research Cooperative.

References

Baig, M.N. and W. Tranquillini. 1976. Studies on upper timberline: morphology and anatomy of Norway spruce *Picea abies* and stone pine *Pinus cembra* needles from various habitat conditions. Can. J. Bot. 54:1622–1632.

Baig, M.N. and W. Tranquillini. 1980. The effects of wind and temperature on cuticular transpiration of *Picea abies* and *Pinus cembra* and their significance in desiccation damage at the alpine treeline. Oecologia 47:252–256.

Cochrane, P.M. and R.O. Slatyer. 1988. Water relations of *Eucalyptus pauciflora* near the alpine tree line in winter. Tree Physiol. 4:45–52.

DeHayes, D.H., C.E. Waite, M.A. Ingle and M.W. Williams. 1990. Winter injury susceptibility and cold tolerance of current and year-old needles of red spruce trees from several provenances. Can. J. For. Res. In press.

DeLucia, E.H. and G.P. Berlyn. 1984. The effect of increasing elevation on leaf cuticle thickness and cuticular transpiration in balsam fir. Can. J. Bot. 62:2423–2431.

Friedland, A.J., R.A. Gregory, L. Kärenlampi and A.H. Johnson. 1984. Winter damage to foliage as a factor in red spruce decline. Can. J. For. Res. 14:963–965.

Gates, D.M. 1968. Transpiration and leaf temperature. Ann. Rev. Plant Physiol. 19:211–238.

Hadley, J.L. and W.K. Smith. 1983. Influence of wind exposure on needle desiccation and mortality for timberline conifers in Wyoming, USA. Arc. Alp. Res. 15:127–135.

Hadley, J.L. and W.K. Smith. 1986. Wind effects on needles of timberline conifers: seasonal influence on mortality. Ecology 67:12–19.

Hadley, J.L. and W.K. Smith. 1987. Influence of krummholz mat microclimate on needle physiology and survival. Oecologia 73:82–90.

Hadley, J.L., A.J. Friedland, G.T. Herrick and R.G. Amundson. 1990. Winter desiccation and solar radiation in relation to red spruce decline in the northern Appalachians. Can. J. For. Res. In press.

Hansen, D.H. and L.G. Klikoff. 1972. Water stress in krummholz, Wastach Mountains, Utah. Bot. Gaz. 133:392–394.

Havis, J.R. 1965. Desiccation as a factor in winter injury of Rhododendron. Proc. Amer. Soc. Hort. Sci. 86:764–769.

Hornbeck, J.W. and R.B. Smith. 1985. Documentation of red spruce growth decline. Can. J. For. Res. 15:1199–1201.

Johnson, A.H. and T.G. Siccama. 1983. Acid deposition and forest decline. Env. Sci. Tech. 17:294A–305A.

Johnson, A.H., A.J. Friedland and J.G. Dushoff. 1986. Recent and historic red spruce mortality: evidence of climatic influence. Water Air Soil Pollut. 30:319–330.

Kincaid, D.W. and E.E. Lyons. 1981. Winter water relations of red spruce on Mount Monadnock, New Hampshire. Ecology 62:1155–1161.

Kramer, P.J. 1983. Water relations of plants. Academic Press, Boston.

Larcher, W. and R. Seigwolf. 1985. Development of acute frost drought in *Rhododendron ferrugineum* at the alpine timberline. Oecologia 67:298–300.

Marchand, P.J. 1972. Wind and the winter-exposed plant. Rhodora 74:528–531.

Marchand, P.J. and B.F. Chabot. 1978. Winter water relations of tree-line plant species on Mt. Washington, New Hampshire. Arc. Alp. Res. 10:105–116.

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

Reiners, W.A. and G.E. Lang. 1979. Vegetational patterns and processes in the balsam fir zone, White Mountains, New Hampshire. Ecology 60:403–417.

Sakai, A. 1968. Mechanism of desiccation damage of forest trees in winter. Contr. Inst. Low Temp. Sci. Ser. B 15:15–35.

Sakai, A. 1970. Mechanism of desiccation damage of conifers wintering in soil-frozen areas. Ecology 51:657–664.

Scott, J.T., T.G. Siccama, A.H. Johnson and A.R. Breisch. 1984. Decline of red spruce in the Adirondacks, New York. Bull. Torrey Bot. Club 111:438–444.

Siccama, T.G. 1974. Vegetation, soil, and climate on the Green Mountains of Vermont. Ecol. Monog. 44:325–349.

Siccama, T.G., M. Bliss and H.W. Vogelmann. 1982. Decline of red spruce in the Green Mountains of Vermont. Bull. Torrey Bot. Club 109:162–168.

Slatyer, R.O. 1976. Water deficits in timberline trees in the Snowy Mountains of south-eastern Australia. Oecologia 24:357–366.

Smith, W.K. and G.A. Carter. 1988. Shoot structural effects on needle temperatures and photosynthesis in conifers. Amer. J. Bot. 75:496–500.

Sokal, R.R. and F.J. Rohlf. 1981. Biometry, 2nd Edn. W.H. Freeman and Co., New York.

Sowell, J.B., D.L. Koutnik and A.J. Lansing. 1982. Cuticular transpiration of whitebark pine *Pinus albicaulis* within a Sierra Nevadan timberline ecotone, USA. Arc. Alp. Res. 14:97–103.

Tibbals, E.C., E.K. Carr, D.M. Gates and F. Kreith. 1964. Radiation and convection in conifers. Amer. J. Bot. 51:529–538.

Tranquillini, W. 1976. Water relations and alpine treeline. *In* Water and Plant Life. Eds. O.L. Lange, L. Kappen and E.-D. Schulze. Springer-Verlag, New York. pp 473–491.

Tranquillini, W. 1979. Physiological ecology of the alpine treeline. Springer-Verlag, New York.

Tranquillini, W. 1982. Frost-drought and its ecological significance. *In* Physiological Plant Ecology II. Eds. O.L. Lange, P.S. Nobel, C.B. Osmond and H. Ziegler. Springer-Verlag, New York, pp 379–400.

Turner, N.C. 1981. Techniques and experimental approaches for the measurement of plant water status. Plant Soil 58:339–366.

Wardle, P. 1981. Winter desiccation of conifer needles simulated by artificial freezing. Arc. Alp. Res. 13:419–423.

White, W.C. and C.J. Weiser. 1964. The relation of tissue desiccation, extreme cold, and rapid temperature fluctuations to winter injury of American Arborvitae. Amer. Soc. Hort. Sci. 85:554–563.

Zimmerman, M.H. and C.L. Brown. 1971. Trees: structure and function. Springer-Verlag, New York.