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Cytopathological and external observations on red spruce (Picea rubens Sarg.) needles damaged in winter in Vermont

Lauri Kärenlampi & Andrew J. Friedland

TIIVISTELMÄ: SOLUPATOLOGISIA JA ULKOISIA HAVAINTOJA PUNAKUUSEN (PICEA RUBENS SARG.) NEULASTEN TALVITUHOISTA VERMONTISSA

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The red spruce population in the Green Mountains in Vermont has shown foliar deterioration that has not yet been fully explained. The most characteristic needle injuries of the sensitive trees appear in late winter when the first-year needles turn brown. The cytopathological and external observations on the symptoms support the interpretation that winter stress triggers the damage. It is possible that some anthropogenic stress factors (components of acid deposition or ozone?) and/or natural factors predispose the trees to the damage.

Vermontin vuorilla Koillis-Yhdysvalloissa kasvava punakuusi kärsii tuhoista, joiden syyt liitetään usein ilman epäpuhtauksiin. Vaurioiden voimakkuus vaihtelee suuresti puuyksilöiden kesken. Herkkien puiden neulasoireiden havaittiin kehittyvän lopputalvella, jolloin etenkin uusimmat neulaset muuttuivat ruskeiksi. Solupatologiset ja ulkonaiset havainnot tukivat tulkintaa, että kysymyksessä on talvistressin laukaisema tuho, joka muistuttaa paljon Suomessa talven 1984–85 jälkeen havaittua. Vermontissa tuho näyttää toistuvan usein ja populaatio on taantumassa. Täten talvituholle herkistävänä tekijänä voi olla esim. vuorilla havaittu happaman laskeuman joku osatekijä tai otsoni.

Keywords: conifer needles, air pollution, symptoms, winter stress
ODC 174.7 *Picea rubens* +416.1+422.1+181.221.1+425+181.45+(74)

Authors' addresses: *Kärenlampi:* University of Kuopio, P.O.Box 6, SF-70211 Kuopio, Finland; *Friedland:* Environmental Studies Program, Dartmouth College, 103A Nathan Smith Bldg., Hanover, N.H. 03755, USA.

1. Introduction

The deterioration of red spruce (*Picea rubens* Sarg.) has been the subject of several studies, summarized by Johnson and Siccama (1983). The major visible foliar symptoms are loss of needles from the tips of the branches and from the apex of the crown without pronounced chlorosis or nutrient deficiency.

In the dieback of an individual tree, the symptoms are most apparent in the needles. These symptoms have been briefly described by Friedland et al. (1984) but otherwise a detailed analysis of the injured needles ap-

pears to be lacking. Injuries of the needles can reflect events which have happened earlier in other parts of the tree or they can be the very starting point of the syndrome. In either case, observations on the condition of the mesophyll cells of red spruce needles are important. Here we present external symptom description with cell and tissue structure observations made with light and electron microsopy of the pathological changes in needles of red spruce growing at high and low elevations in the Green Mountains of Vermont (VT), north-eastern USA.

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2. Materials and methods

21. Study sites

Samples from the high elevation site were collected at 1000-m elevation on the west slope of Camels Hump, Huntington, VT. Vegetation, soils and climate of Camels Hump have been described in detail by Siccama (1974). The study area has not been burned, cut or subject to major human disturbance since presettlement times (Siccama 1974). Overstory basal area (>10 cm dbh) determined by Siccama et al. (1982) is 25–30 m^2 ha^{-1}. Between 1965 and 1977, basal area of red spruce decreased by 50 % at 850–1100 m elevation on the west slope (Siccama et al. 1982). Many dead and deteriorating red spruce have been observed on Camels Hump (Johnson and Siccama 1983). In the months of the sampling for this study, needle browning of much of the newest growth was observed and has been related to winter injury (Friedland et al. 1984).

The second study area was a native red spruce stand at 460-m elevation at the base of a talus slope on South Mountain, Bristol, VT. This low-elevation spruce stand, hereafter called the Bristol site, is mixed with white pine (*Pinus strobus* (L.)Mill.). The Bristol site is micro-climatically controlled by cold air drainage from the talus slope. The total area of red spruce stand is approximately 2 to 3 ha. While extensive browning of newest foliage was noted at Camels Hump during the spring and summer of 1984, virtually none was observed at Bristol.

22. Methods

On Camels Hump foliage was collected from 4 visibly deteriorating and 4 visibly healthy trees on 7 April, 1984 and from 5 visibly deteriorating and 5 visibly healthy trees on 28 August and 5 November, 1984. At Bristol foliage was collected from 5 visibly healthy trees on 28 August and 5 November, 1984.

Foliage was collected approximately 5–7 m above the ground surface from mature red spruce trees only. Foliage was immediately placed in plastic bags and was stored in a wet ice cooler within 2 hours. Samples were shipped in a cooler as air freight to the University of California, Los Angeles, where preparation for microscopy was begun within 48 hours for the 7 April collection and within 24 hours for the latter two collections. In the April collection, the following needle categories of both visibly deteriorating and visibly healthy trees were prepared for microscopy: 1st-year needles (elongation began in 1983, about 10 months old), 2nd-year needles, on which longitudinal sections were also made, and 6th-year needles. From the 1st-year needles of the visibly deteriorating trees, the partially green portion of the needle was sampled. In the August and November collections 1st-year needles (emerged in 1984) and the 2nd-year needles (emerged in 1983) were studied microscopically.

For microscopy, selected needles were cut with a razor blade in a drop of 2 % glutaraldehyde in 0.1 M Na-phosphate buffer (pH 7) and were fixed for 12–20 hours. One percent OsO_4 (osmiumtetraoxide) in the buffer was used for a 6-hour postfixation. Dehydration was done in graded ethanol series followed by propylene oxide and embedding in Medcast epoxy resin. All samples were stored below 4 °C until the beginning of the dehydration. 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. Visible symptoms were observed with a magnifying lens or binocular microscope and recorded.

3. Results and discussion

31. External symptoms

From the first sampling on Camels Hump in April 1984, the 1st-year needles of the deteriorating trees were badly injured. On the most heavily injured branches, almost all needles were light brown and the buds were withered. The browning showed no regular pattern; it was visible on the tip, base, middle portion, or along one side of the needle. In the most badly injured branches, the growth of some previous years had withered earlier, probably during the first winter. New growth had started from additive buds and had replaced the earlier branch leaders. Therefore, the general appearance of the branch was short and bushy.

Only a few of the older needles of the visibly deteriorating trees showed similar browning. Instead, they showed grey flecks on the upper surfaces. These flecks were successively larger and more numerous in the older needles.

There was very little browning on the 1st-year needles from the healthy trees on Camels Hump. Surface flecks were present on 1st-year needles but were more abundant on older needles, as we observed on the visibly deteriorating trees. The longest needle retention time observed on the sample branches for healthy and deteriorating trees was 10 years.

The upper-surface flecks resemble those described as winter flecks on some pines by Miller and Evans (1974). Similar winter flecks are common on many pine species in mountain areas of California (unpublished observations, L. Kärenlampi) and they may be caused by rim-ice formation or by the effects of sun light; they have no apparent association with air pollution or with the general health of the tree. The abscission of the needles is not accelerated by the flecks that appear in the winter only.

The damage to red spruce has the characteristic that the 1st-year needles are the most badly injured. In Finland, many winter injury symptoms in conifers were evident after the very cold and long winter of 1984–85. The browning of the previous summer's needles was a typical symptom of winter damage both in many introduced pine species and in Norway spruce. Correspondingly, some individual trees were found sensitive while some others remained without symptoms. Also the browning of the needles was similarly without any clear pattern.

Curry and Church (1952) have described winter damage to many coniferous species, and especially to red spruce, throughout northern New York state. Unfortunately, they did not report on the possible differences between the youngest and the older needle classes, and we do not know if the recently-observed damage is similar. One apparent difference is that in the present case, other conifers do not show synchronous symptoms of damage. There may be predisposing or inciting factors to which red spruce is particularly sensitive.

Fig. 1. Part of a disintegrating (dead) mesophyll cell of a 1st-year needle of a visibly deteriorating tree from Camels Hump, April 7, 1984. In the chloroplast (chl), the outer membrane is disrupted (arrow) and the stroma is strongly swollen. Thylakoids are swollen and dispersed. Plasmalemma has separated (asterisk) from the cell wall (cw) × 12200.

Fig. 2. Mesophyll cells of a 1st-year needle of a visibly deteriorating tree from Camels Hump, April 7, 1984. The cell in the upper right hand corner is disintegrating, with recognizable remnants of chloroplast (chl) and nucleus (n). The cell to the left represents the depressed condition where electron dense deposits cover the poorly resolved cytoplasm which is partly separated (asterisk) from the cell wall (cw). The cell in the lower right hand corner has collapsed totally. × 3 300.

Fig. 3. Part of a depressed cell of a 1st-year needle of a visibly deteriorating tree from Camels Hump, April 7, 1984. The electron dense layer (presumably tannin) covers the remnants of the protoplast: central vacuole (cv), cell wall (cw). × 32 100.

Fig. 4. Part of a depressed cell of a 2nd-year needle of a healthy tree from Camels Hump, April 7, 1984. Membrane structures have become very indistinct and only groups of osmiophilic globules (og) within chloroplasts are still visible. Deposits on the vacuole side of the tonoplast appear vesiculated. × 6 700.

Fig. 5. Healthy cell of a 1st-year needle of a healthy tree from Camels Hump, April 7, 1984. Central vacuole (cv) contains granular material (presumably tannin deposits). Cytoplamic vacuoles (cv) and lipid droplets (ld) are also visible. × 3 300.

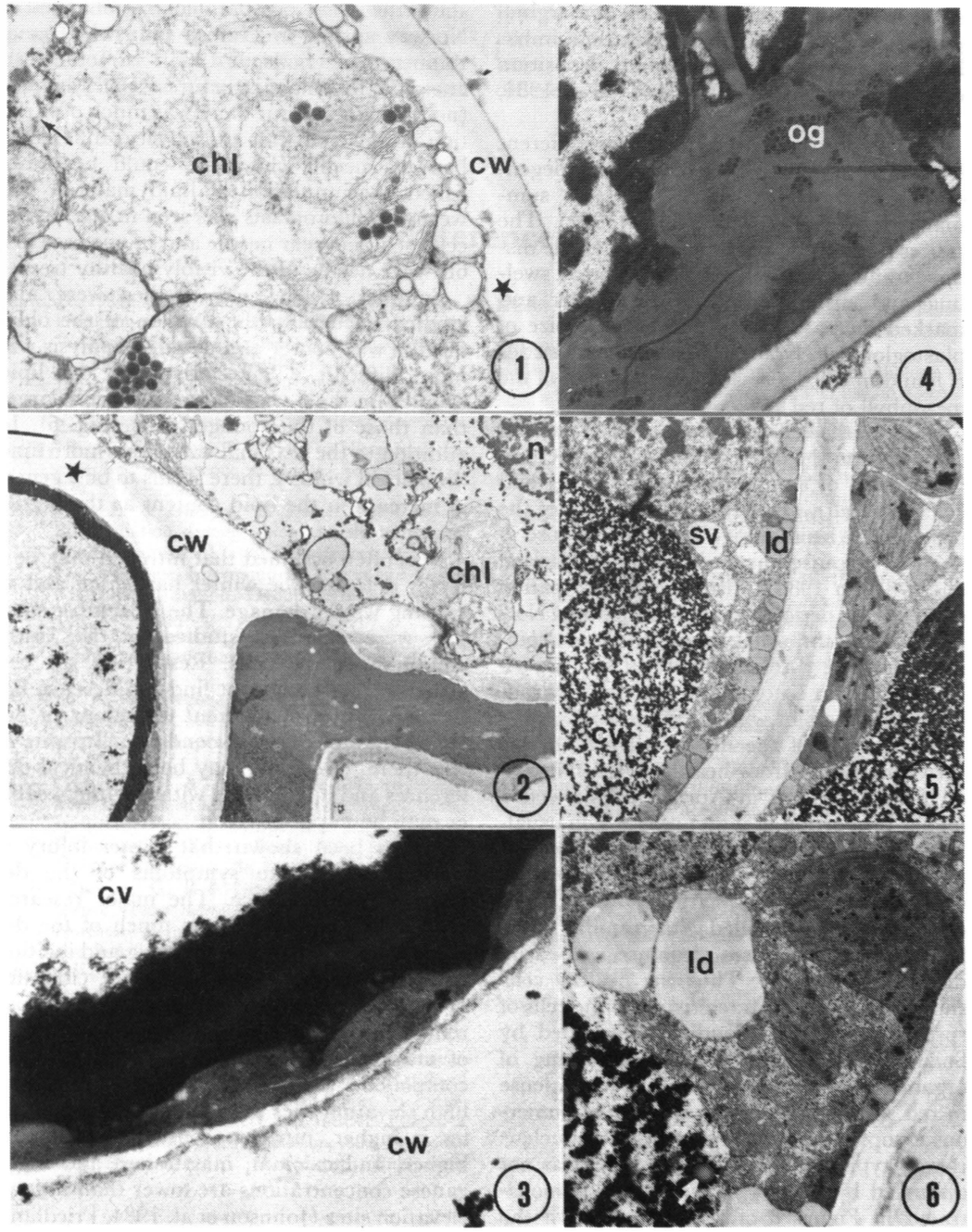
Fig. 6. A healthy cell of a 6th-year needle of a healthy tree from Camels Hump, April 7, 1984. One apparent difference from the younger cells is the numerous and large lipid droplets (ld). Small droplets (white arrow) occur in the central vacuole of the cell. × 4 500.

32. Microscopical observations

Microscopy of the needles sampled in April revealed that most of the mesophyll cells of the 1st-year needles of the symptomatic trees were disintegrating (Figs. 1 and 2). Cell organelles were greatly swollen, distinction between cytoplasm and central vacuole was lost, and cell turgidity was lost. Usually membranes other than the tonoplast were easily discernible. Cell injuries of young Norway spruce that were strongly fertilized with nitrogen and showed winter damage, were similar disintegrations (experiment made in Kuopio in winter 1986–87). The disintegrating cells resemble also those reported in Norway spruce by Soikkeli (1978) who assumed that the destruction was caused by cold weather following a warm spell early in spring. The frost damage easily destroys the tonoplast and the distinction between cytoplasm and central vacuole (cf. Ziegler and Kandler 1980).

Many of the remaining cells, especially in the inner mesophyll showed a type of "depressed" condition (Figs. 3 and 4) that occurs in the healthier needles, too. Poorly resolved cytoplasm and cell organelles were covered from the vacuolar side by a dark electron dense layer. Within the cytoplasm, lipid accumulations were visible. The chloroplasts were reduced in size and within groups of chloroplasts it was difficult to distinguish individuals. With the light microscope, the depressed cells were recognized by the dark, thin protoplast covered by the dark layer along the tonoplast. The background color of the central vacuole was darker than in healthy cells and plasmolysis was common.

The depressed cells are similar to the injured cells described by Soikkeli and Tuovinen (1979), Soikkeli (1981) and Soikkeli and Kärenlampi (1984). This type of slow cell degeneration seems to be typical in many pine and spruce species. The authors cited above suggest that the cause may be chronic air pollution or even strong nitrogen fertilization in the boreal climate. In red spruce, this cell condition had started to develop in some cells by the first growing season. The phenomenon occurs to some extent in the visibly healthier trees, too. The phenomenon



may be a natural reaction through which the perennial needle 'preserves' some cells which, for some reason, cannot stay functional. The process may be denaturation of proteins by the contents of the central vacuole. In the case of red spruce, it is not known what factors trigger the development of the depressed condition. The shorter growing period and colder temperatures that limit the elevational and geographic range of the

species (montane red spruce are a marginal population, Wright 1955) and nutrient imbalances caused by anthropogenic deposition can be suspected (cf. Friedland et al. 1984, 1985).

The depressed cell condition is different from the common pattern of plant cell degeneration and death which has been summarized by Butler and Simon (1971). The process which they outlined includes the disappearance of the chloroplast stroma, swelling and disintegration of thylakoids and marked increase in the number and size of plastoglobules. None of these characteristics is found in the depressed cell condition of the mesophyll of red spruce.

Some of the cells appeared to be functional as judged on the basis of the intact structure. Other cells of the symptomatic needles had collapsed cell walls with the remnants of the protoplasm inside (Fig. 2). The collapse is likely to be caused by desiccation (cf. Carlson and Gilligan 1983). Also in cold desiccation experiments performed with branches of Norway spruce, the collapse was the most common response (preliminary results of experiments made in Kuopio in controlled environment chambers in winter 1986–87).

Microscopy of the mesophyll cells of the 1st-year needles from healthy trees sampled on Camels Hump in April 1984 showed a higher proportion of intact cells which usually had rounded nuclei with plenty of organelles (chloroplasts, mitochondria, microbodies, cytoplasmic vacuoles) around them. The central vacuole was filled with granular material and the cytoplasm structure was easily discernible (Fig. 5). Thus the healthy cells showed the same characteristics as the cells of spruce in a winter condition described by Soikkeli (1978). Probably the clumping of organelles around the nucleus is less intense in red spruce and the appearance of numerous cytoplasmic vacuoles around the nucleus is very typical. This latter character was not discussed by Soikkeli (1978) but is demonstrated in Figure 8 of that paper. Both the disintegrating and the depressed cell types occurred in the healthier needles, too, but their proportion was small. The disintegrating cells were most often found in the outer mesophyll and the depressed cells in the inner mesophyll.

The mesophyll cells of red spruce did not show the same cytopathological changes as Norway spruce in Finnish industrieal environments (cf. Soikkeli 1981). In some instances the thylakoid structure was very simple (no thick grana) but there was much of variation in this character and no clear differences between needle categories could be established. Accumulation of lipid material between the chloroplasts was seen in one case in cells of a 2nd-year needle and in one case in a 6th-year needle of the visibly healthy trees.

Samples of the old needles were also studied. Generally the fixation of the older needles was poorer and detailed analysis was more difficult. Characteristically the lipid droplets in the 6-year-old needles were larger than those of the younger cells (Fig. 6). In addition to the seasonal variation (more lipid droplets in winter), there seems to be a general increase in the lipid content as the needle becomes older.

It is often assumed that nitrogen may be a factor delaying the winter hardening and so causing winter damage. The November samples were especially studied for the winter condition of the cells. Respecting the cell structure, we could not find a difference between samples of different elevations or between trees of different condition. In spite of this there, of course, may be bichemical differences and interactions with autumn weather may be important, too.

It has been shown that winter injury is strongly related to symptoms of the deteriorating red spruce. The major research problem remaining is how much of the deterioration is due to predisposing and inciting factors which may be natural (e.g. climatic) or anthropogenic. The deterioration is apparent at the higher elevations where deposition of nitrogen and many other anthropogenic components is high. Correspondingly, at the high elevation sites the sulfur content of needles is higher, nitrogen content tends to be higher, and calcium, magnesium and manganese concentrations are lower than at low-elevation sites (Johnson et al. 1984, Friedland et al. 1987, 1988). These variations in nutrient content resemble those observed in damaged conifers in Germany (e.g. Knabe 1984). These differences in foliar chemistry, particularly inorganic nutrient deficiences, may be associated with decreased cold or desiccation hardiness (Baule 1984a, b).

The comparisons of the decline of red spruce with that of Central European *Abies alba* and *Picea abies* are interesting but it is obvious that the two diseases are different. Red spruce does not show such yellowing or crown thinning syndrome as the European trees and also the cytological changes are different (cf. Parameswaran et al. 1985).

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