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Morphological Changes in Leaves of Residual Western Hemlock After Clear and Shelterwood Cutting

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ABSTRACT. The change in microclimate associated with clear and shelterwood cutting had marked effects on the leaves of residual western hemlock trees. In a new clearcutting, old needles abscised prematurely and needles that formed during the first season of exposure were smaller than normal, apparently because of water stress. Needles formed in the second season had thicker palisade mesophyll, a smaller ratio of surface area to weight, and more stomata per unit surface area. Leaves that had developed in the shade and were later exposed showed a slight increase in thickness, probably because of increased palisade mesophyll development. These changes in leaf area and structure were toward a configuration which was more efficient in utilization of light and water in a clearcutting. Hemlock saplings left in a shelterwood suffered less needle loss and mortality, but they still developed needles adapted to full sunlight, suggesting a shelterwood as a beneficial treatment for understory hemlock. FOREST SCI. 23:195–203.

ADDITIONAL KEY WORDS. Palisade mesophyll, *Tsuga heterophylla*, microclimate, stomatal frequency, ratio of surface area to weight.

WESTERN HEMLOCK (*Tsuga heterophylla* (Raf.) Sarg.) in much of western Oregon is a climax species, which develops as an understory in old-growth forests of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). Typically, small hemlock are destroyed during logging, either in the process of removing the large volume of old-growth Douglas-fir or in the slash fires designed to reduce fuel and control fire danger. Recently, however, hemlock has been recognized as a valuable source of wood fiber, and a coastal hemlock forest in Oregon was found to be among the most productive in the world (Fujimori 1971). The possibility of managing for growth and preservation of understory hemlock by careful removal of the overstory led us to investigate one aspect of hemlock's response to overstory removal.

Hemlock trees exposed to a new microclimate after initial development in the shelter of a stand must make rapid adjustments to survive. First, transpiration from leaves under greater evaporative demand must be brought into equilibrium with the amount of water the root systems can supply, especially during periods of peak demand. With exposure to higher amounts of radiation, additional layers of palisade mesophyll are required to prevent destruction of chlorophyll (Anderson 1955, Watson 1942, Stover 1944). Such differences between leaves developed in sun and

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shade have long been recognized (Groom 1893, Penfound 1931) in various species.

Our objective was to observe changes in leaf morphology of western hemlock brought about by changes in microclimate after clear and shelterwood cutting. We measured leaf length, width, thickness, surface area, and palisade mesophyll thickness on three age classes of needles to clarify the extent and timing of changes in hemlock foliage brought about by these two common silvicultural manipulations. We also observed plant water potential.

Methods

Study Area.—The study site, a western hemlock/vine maple/Oregongrape habitat type (Dyrness and others 1974), was located on the H. J. Andrews Experimental Forest, about 100 kilometers east of Eugene, Oregon, in the western Cascades vegetation province (Franklin and Dyrness 1973). The area has a 25 percent slope, southern aspect, an elevation of 1,250 meters and a deep Brown Podzolic soil of the Carpenter Series (Dyrness and Hawk 1972).

Before treatment, the area was covered by a uniform 140-year-old Douglas-fir stand with a basal area of 76 m^2 ha^{-1} (327 ft^2 A^{-1}). The stand originated after a fire, which killed most of the older Douglas-fir stand. Before cutting, western hemlock up to 4 m in height were estimated to cover 23 percent of the ground area (Dyrness and Hawk 1972).

Treatments.—An "old" clearcutting, harvested with a high-lead system in 1963 and burned in 1964, served as the first treatment. A few hemlock survived to serve as sample trees in the present study. A "new" clearcutting and a shelterwood cutting were harvested by tractor and high-lead logging in May and June of 1974. The 1974 needles were forming during the same period. All overstory trees were removed from the clearcutting, and 59 percent of the basal area was removed from the shelterwood. We estimated that 95 percent and 50 percent of the residual hemlock had died by the fall of 1974 in the clearcutting and shelterwood cutting, respectively. In mid-May of the following spring, slash was burned on the two recently cut areas. The burn was light in the shelterwood, and many of the surviving residual hemlock were left unharmed. The clearcutting burned more intensely, however, and most of the remaining residual hemlock were killed. A portion of the original stand was left uncut as a control. Thus, four conditions were present for sampling in the fall of 1975: old clearcutting; new clearcutting; shelterwood cutting; and control stand.

Microclimate and Plant Response.—To characterize the different microclimates, we recorded temperature at –20 cm in the soil and at 1 m above ground at the two recently treated areas and in the control stand throughout the 1975 growing season (May through October). Dewpoint temperature was recorded during much of the same period in the stand and new clearcutting. Total daily incoming shortwave radiation was measured in the open with an American Instrument Co. solarimeter. Relative light was determined for the three treatments by exposing ozalid paper light sensors for one entire day on a transect established across the areas as described by Friend (1961) and Emmingham and Waring (1973).

Predawn moisture potential of three hemlock saplings between 1 and 2 m in height were sampled in each treatment six times, starting June 5 and ending on September 30, 1975, to characterize the moisture status of trees in the treated areas (Scholander and others 1965, Waring and Cleary 1967).

Leaf Morphology.—In the fall of 1975, samples of leaves were collected from the last three age classes (those formed the year before treatment, the season of treat-

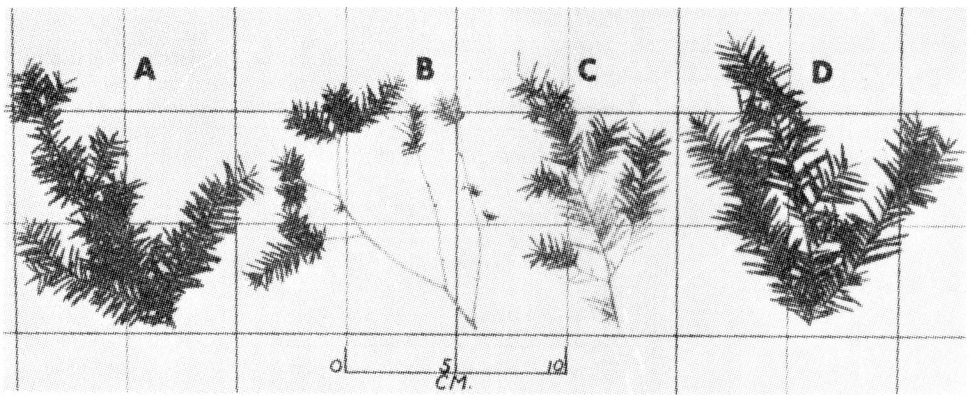


FIGURE 1. Comparisons of western hemlock branches taken from: (A) old, established clearcutting; (B) new clearcutting; (C) shelterwood; and (D) control stand.

ment, and the year after treatment). Samples of both large and small needles were taken from the outermost branch on the south-facing side of the crown at about 1.5 m above the ground. All samples were immediately deposited in a formalin fixing solution to preserve their natural form. Length and width of needles was determined under a 7-power dissecting microscope. Leaves were then imbedded in paraffin and sectioned using standard plant microtechnique (Johansen 1940). Thickness, width, and circumference were determined under magnification on cross sections taken midlength of the needle. The thickness and the number of rows of palisade mesophyll were also determined.

The ratio of surface area to weight was determined on a second sample of leaves collected with the first. These samples were refrigerated in moisture proof bags until the projected surface area could be measured with the Licor surface area meter (Running 1976). Total (all-sided) leaf area was computed by multiplying projected (one-sided) leaf area by the ratio of circumference to width (Drew and Running 1976). After the same leaves were weighed, the total surface area was used to compute the ratio of surface area to dry weight.

Finally, the number of stomata per unit area, number of rows of stomata, and width of each stomatal band were measured on large leaves from the control stand and old clearcutting with the aid of an epi-illumination objective.

The measurements of the leaves were submitted to three-factor analysis of variance to determine whether variation was associated with treatment, age of needle, or needle size.

RESULTS

Microclimatic.—As a result of silvicultural treatments, the microclimates of shelterwood and clearcut areas changed. Average air temperature during the day in the clear and shelterwood cuttings was about 3°C greater than that in the control stand during the summer months. Maximum temperature in the open during the day rose an average of 4.6°C above that in the control stand. Night minimum and average night temperatures were within 1.6°C at all areas. Soil temperature at 20 cm below the surface averaged 18.8°C in the new clearcutting, 13.9°C in the shelterwood cutting, and 12.3°C in the control stand.

Total incoming shortwave radiation in the clearcutting averaged 423 cal cm^{-2} day^{-1} during the period from July 8 to September 20, 1975. On a typical day in

TABLE 1. Mean dimensions of hemlock needles.[1]

Variable affecting needle dimensions	Length	Width	Thickness	Ratio of width to thickness	Palisade mesophyll thickness	Ratio of surface area to weight
	mm	*mm*	*mm*		*mm*	*cm² gm⁻¹*
A. Needle size						
Large	14.0 a	1.77 a	0.452 a	4.0 a	0.097 a	—
Small	7.7 b	1.53 b	.444 a	3.6 a	.103 a	—
B. Year of formation[2]						
1973	16.9 b	1.81 a	.380 a	4.8 a	.076 a	127 a
1974	14.6 a	1.93 a	.387 a	5.0 a	.081 a	149 b
1975	14.6 a	1.80 a	.355 a	5.1 a	.065 a	235 c
C. Treatment (1975 needles)[2]						
Control stand	14.6 a	1.80 a	.355 b	5.1 b	.065 b	235 b
Shelterwood cutting	14.2 a	1.76 a	.520 a	3.4 a	.117 a	202 a
New clearcutting	15.3 a	1.76 a	.498 a	3.5 a	.099 a	199 a
Old clearcutting	9.8 b	1.86 a	.518 a	3.6 a	.105 a	135 c
D. Treatment (1973 needles)[2, 3]						
Control stand	16.9 a	1.81 b	.380 a	4.8 a	.076 a	127 a
Shelterwood cutting	16.7 a	1.98 a	.406 a	4.9 a	.078 a	122 a
New clearcutting	12.2 b	1.50 c	.409 a	3.6 b	.088 a	105 b
Old clearcutting	16.0 a	1.86 ab	.581 b	3.2 b	.139 b	92 c

[1] Means followed by the same letters were not statistically different at the 5 percent level of probability in a Duncan's Multiple Range test (Li 1957).

[2] Means presented in B, C, and D are for large needles.

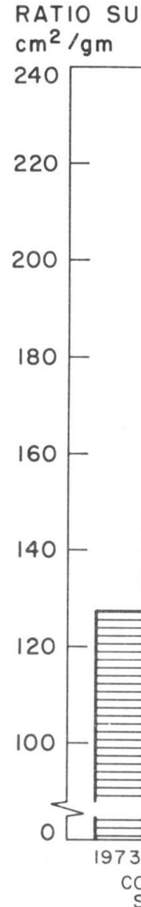
[3] Note that the means for the old clearcutting are for leaves developed in the open but the others formed in the shade. Those in the clear and shelterwood cutting were then exposed to a different microclimate.

that period, the forest floor in the shelterwood cutting received 27 percent and the control received 3 percent of the radiation in the open.

During 21 representative days in June, July, and August, dewpoint temperature averaged only 1.6°C less in the control stand than in the new clearcutting. Evaporative demand, as expressed by vapor pressure deficit, averaged 1.6 mb less in the control stand, and maximum deficit averaged 2.1 mb less.

Water Potential.—Means and standard deviations for six predawn observations of xylem sap potential (Scholander and others 1965, Waring and Cleary 1967) in the control stand, shelterwood, and old clearcutting were –5.5 ± 1.9, –4.9 ± 1.5, –5.5 ± 1.7 bars, respectively. Minimum sap potentials, recorded at the end of September, were –8.2 bars in the control stand, –6.1 bars in the shelterwood, and –7.4 bars in the old clearcutting. None of these differ significantly from the others.

Leaf Area.—Understory hemlock trees exposed to a more severe microclimate dropped older needles (Fig. 1b), leaving an open crown. Trees in the open lost over half of their needle area. Trees in the shelterwood retained most of the older foliage, but older needles become chlorotic after a year and appeared destined for premature abscission (Fig. 1c). In contrast, hemlock already adjusted to conditions in the old clearcutting had thick full crowns (Fig. 1a) and a greater leaf area than trees of similar stature in the control stand (Fig. 1d).



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.103 a	—
.076 a	127 a
.081 a	149 b
.065 a	235 c
.065 b	235 b
.117 a	202 a
.099 a	199 a
.105 a	135 c
.076 a	127 a
.078 a	122 a
.088 a	105 b
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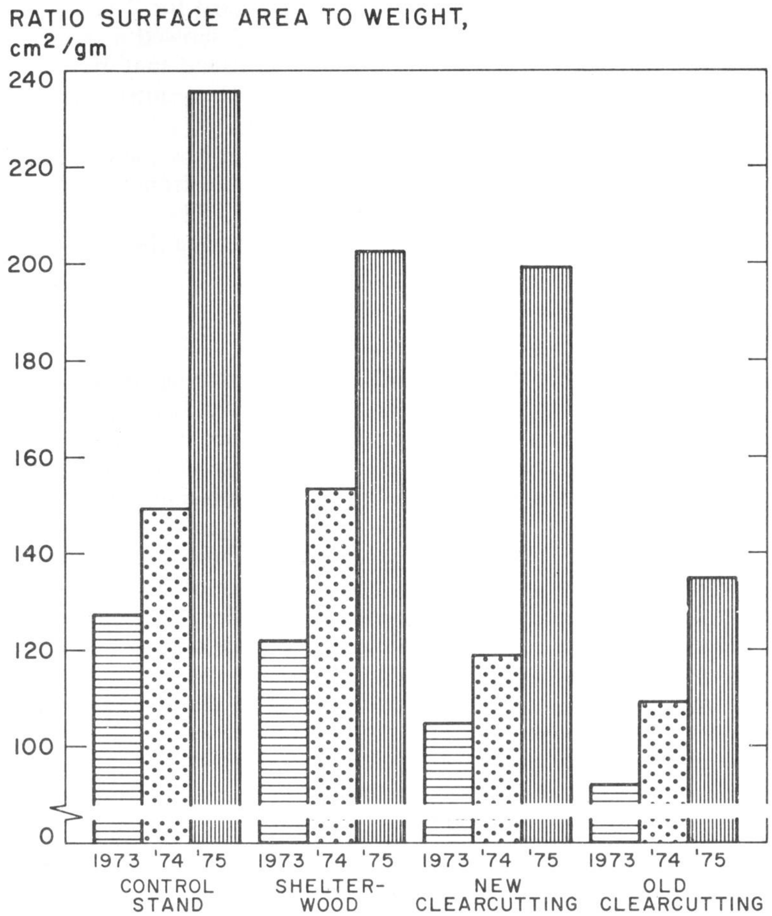


FIGURE 2. Ratios of surface area to weight in 1975 for three age classes of western hemlock needles under four preconditioning regimes. The shelterwood cutting and new clearcutting were completed in June 1974.

Effect of Size Class, Age, and Treatment on Needle Morphology.—Hemlock has two distinct sizes of needles interspersed along each branch. The large needles were nearly twice as long, but only slightly wider than the small needles (Table 1A). The large leaves were not significantly thicker nor did they have a thicker palisade mesophyll than small leaves.

The most striking change with age was in the ratio of surface area to weight (Table 1B). For example, in the old clearcutting, the surface ratio was 135 (cm^2 g^{-1}) for newly formed needles and 92 for 3-year-old needles, a reduction of 70 percent. In the control stand, the reduction was 54 percent. A high correlation of size to age was not apparent (that is, leaves did not expand or shrink after formation). Age and treatment differences reported in Table 1B, C, and D, are for large needles.

Treatment had a significant effect on all morphological factors when tested by analysis of variance. Leaves that developed in the shade were thinner, had a greater ratio of width to thickness, thinner palisade mesophyll, and a greater ratio of surface area to weight than those developed in full sunlight (Fig. 2, Table 1C). Those in the shelterwood cutting were intermediate in these characteristics.

Leaves that developed in shade but were then exposed for 2 years (Table 1D) (for example, 1973 leaves from the new clearcutting) showed a trend toward the characteristics of needles developed in the sun. The trend may be brought about by increased development of palisade mesophyll, which results in thicker needles and lower ratios of surface area to weight (Table 1D).

The number of stomata per mm^2, number of stomatal rows, and the width of the stomatal band (mm) averaged 227, 8, and 2.8 for needles from the old clearcutting and 166, 6, and 2.2 for those from the control stand. Thus, a leaf 14 mm long grown in sun wauld have about 17,800 stomata, and a leaf of the same length grown in shade would have only 10,200.

Discussion

Perhaps the most striking changes in the microclimate associated with the clear and shelterwood cutting were marked increases in light intensity and in soil temperature under the blackened soil surface. Wind changes were not measured. Although the changes in air temperature and evaporative demand were smaller than expected for the average day, the effects on transpiration could be substantial over the length of the growing season.

Observation of hemlock trees exposed to the new microclimate suggest that trees respond by changes in leaf area in several ways: older needles are shed; needles formed under stressed conditions are considerably smaller; the ratio of surface area to weight is lower in newly formed needles; the ratio of surface area to weight of previously formed needles is reduced slightly.

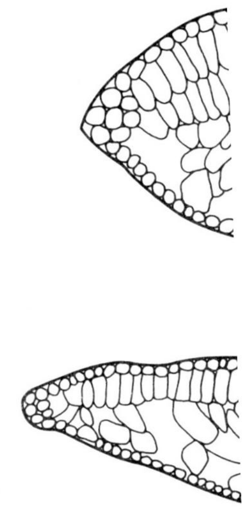
Hemlock trees exposed to the microclimate of a clearcutting responded by dropping older needles. Severe water deficits probably resulted from an inability of newly exposed shade leaves to close their stomata (Keller and Tregunna 1976). Many residual hemlocks did not survive this initial stress. A similar pattern was evident in the shelterwood; however, fewer needles were lost from stress conditions and fewer trees died.

We suggest no functional differences between large and small needles because they differ mainly in length and width, not in thickness of palisade mesophyll nor in number of stomata per unit area.

Adjustments in New Needles.—Leaves formed in the new clearcutting during the summer of treatment were only half the length of those formed the previous year, reflecting stress conditions during the period of formation. These needles were typical sun leaves, however, with a double row of palisade mesophyll. In the second summer after treatment, the palisade mesophyll developed in needles on shelterwood trees was nearly as thick as that formed in the old clearcutting even though light intensity was only about ¼ of that in the open. The studies of Aussenac (1973) in *Picea*, *Abies*, and *Pseudotsuga*, also indicated that conifers respond to higher light intensity by producing an additional row of palisade mesophyll cells. Studies of broad-leaved species (Anderson 1955, Watson 1942) showed an increase in the length of palisade cells.

Because of increased thickness, leaves developed in the open had smaller ratios of width to thickness. Thus, easily measured external factors were correlated with an increase in the functionally important palisade mesophyll. Aussenac (1973) found a similar correlation between ratio of width to thickness and openness of growth condition.

The high ratio of surface area to weight of the leaves in the control stand indicated a broad, shade leaf, and the low ratio in the open indicated a "fat" sun leaf (Fig. 3). The low ratio of leaves formed in the sun indicates less surface area per



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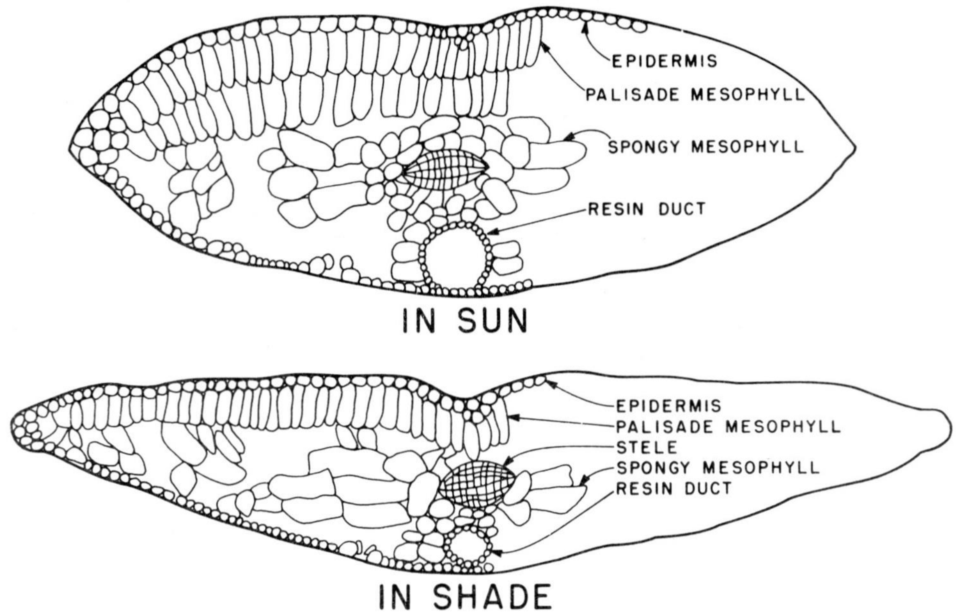

FIGURE 3. Cross sections of typical hemlock needles developed in full sunlight and in the shade of a dense Douglas-fir canopy.

unit of photosynthetic tissue and could result in a more favorable energy balance for the leaf (Gates 1968).

The decrease in the ratio of surface area to weight with age, which was apparent at all four areas (Fig. 2), could result from addition of structural material or from deposition of waste products as suggested by Cole and others (1968). A reduction of nearly 50 percent in this ratio from 1-year-old to 3-year-old leaves in the control stand points up the importance of knowing age distribution in studies where detailed knowledge of leaf surface areas is to be derived from leaf biomass (Whittaker and Neiring 1975, Gholz and others 1976). McLaughlin and Madgwick (1968) and Smith (1972) indicated that accurate determination of leaf area requires knowledge of leaf age, habitat, and crown position.

The greater number of stomata found in sun leaves of hemlock would lead to more CO_2 diffusion into the leaf and transpiration from the leaf, which would increase evaporative cooling. Unlike newly exposed shade leaves, sun leaves were adapted to control water loss during periods of high evaporative demand (Running 1976).

Measures of xylem sap potential throughout the growing season indicated that with the above adjustments, and perhaps others, such as increased thickness of cuticular wax, the residual hemlock maintained a favorable water balance within a year of treatment. An increase in root surface area could contribute to a favorable water balance; however, Dr. J. Zaerr (personal communication) found root-regenerating capacity greatly reduced by increased light intensity and loss of foliage.

Adjustments in Already Formed Needles.—Evidence for adjustments in needles formed before cutting is not as strong as for newly forming needles, nor are the changes as complete. If we can assume that the needles formed in the understory before cutting were the same as those in the control plot, then certain changes have occurred in the needles formed in 1973 and exposed in 1974 (Table 1D).

The changes were most apparent in the new clearcutting, where the palisade mesophyll thickness, leaf thickness, and ratios of both width to thickness and surface area to weight were intermediate between those developed in the stand and those developed in the open. A similar result was shown by Watson (1942), who observed development of palisade tissue in English ivy after plants developed in shade were moved into full sun.

Implications.—These results imply that residual western hemlock seedlings and saplings may be saved in some areas by using a shelterwood rather than a clearcutting system. A shelterwood system should allow 3 to 5 years for development of sun leaf characteristics before complete overstory removal. Such a system could have advantages in: reducing the visual impact of overstory removal; reducing the period when site production potential is lost because leaf area of commercial species is low; and conversion of a site from Douglas-fir to hemlock where hemlock is more productive.

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