BG Smith (26)
Roots
Forest canopy
Forest regeneration
Shade

Effect of root competition and shading on growth of suppressed western hemlock (*Tsuga heterophylla*)

E. Jennifer Christy*
Tree Fruit Research Laboratory, U.S. Department of Agriculture, 1104 N. Western Ave., Wenatchee, WA 98801, USA

Keywords: Canopy gap, Light, Old-growth forest, Oregon, Root competition, *Tsuga heterophylla*, Trenching.

Abstract

Factors suppressing the growth of *Tsuga heterophylla*, western hemlock, (40–200 cm tall) were separated into aboveground and belowground components. Canopy manipulation by creating gaps produced approximately a 30–34% increase in the overall amount of light available. Growth of the previously suppressed *T. heterophylla* was increased by minimizing root competition by trenching around individuals and to a much lesser degree by altering the canopy. The combination of the two manipulations did now show a strong synergistic effect.

Introduction

The low elevation, old-growth forests in the western Cascades of central Oregon are currently dominated by Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco, maximum age 250–500 yr] plus a multilayered canopy composed primarily of western hemlock [*Tsuga heterophylla* (Raf) Sarg.], a species dominating climax stands over much of its range (Fowells, 1965). Typically in old-growth stands, 10–30% of the forest floor is covered by dead wood, both snags (upright dead trees) and prostrate logs (Grier & Logan, 1977). At this late stage in succession, no Douglas-fir seedlings survive (Munger, 1940), and the survival of western hemlock seedlings is closely linked to the rooting substratum (Christy & Mack, 1984). Juveniles of western hemlock in these late successional old-growth forests become part of a bank of persistent seedlings (*sensu* Grime, 1979). Such plants may survive for many years in a suppressed condition until favorable environmental conditions promote the resumption of growth.

The objectives of this study were to assess the ability of suppressed *Tsuga heterophylla* to respond when limitations on aboveground and belowground resources were altered experimentally in an old-growth forest stand. Resource availability was changed in two ways: by increasing the amount of light incident on juvenile western hemlock by creating gaps in the canopy and/or by decreasing the amount of root competition by trenching around individuals.

* I thank Greg Helve and Randy Kelley for digging trenches. R. Mack, J. Thompson, J. Franklin, and A. McKee provided useful suggestions throughout the study. I appreciate the comments from the Ecological Discussion Group at Washington State University. This study was supported partially with funds to Oregon State University from the National Science Foundation, as well as the Society of Sigma Xi, and Washington State University.

Methods

Site description

The experiments were conducted in an old-growth forest stand (*sensu* Franklin & Hemstrom, 1981) on the H. J. Andrews Experimental Forest

Vegetatio 65, 21–28 (1986).

(Williamette National Forest) in the Cascade Range, about 64 km east of Eugene, Oregon, USA. Annual precipitation is approximately 2400 mm and average summer rainfall (June, July, August) is about 100 mm (Waring *et al.*, 1978). The study site occurs at 531 m on a northwest facing slope within the *Tsuga heterophylla/Rhododendron macrophyllum-Berberis nervosa* habitat type in the *T. heterophylla* zone (Hawk *et al.*, 1978). Detailed community descriptions have been prepared from several permanent plots in the same habitat type within the Experimental Forest (Hawk *et al.*, 1978).

The experiments were conducted using 80 western hemlock juveniles which were 40–200 cm tall. Juveniles are defined as individuals less than 4 m tall and less than 35 years old. All individuals selected for study showed signs of suppressed growth such as dead branches in the lower part of the canopy, a somewhat horizontal rather than vertical growth of the main bole, or several lateral leaders at the top of the trunk rather than one terminal leader.

Root zone manipulation

Root zones of 40 juvenile western hemlocks were isolated experimentally in the summer of 1979. For 16 juveniles rooted on logs, all other woody individuals rooted on the log within 5 m of the juvenile were cut at the base of their trunks. The 24 western hemlock juveniles rooted in soil were isolated by an encompassing trench which was approximately 1 m in radius from the base of the plant and not less than 0.5 m deep. Trenches were excavated until fine roots were no longer abundant, but generally a 50 to 75 cm level was well below the majority of fine and medium roots (Eis, 1974; Santantonio *et al.*, 1977). The trench was lined with a polyethylene sheet (6 mil) and back-filled. Adventitious shoots from the remaining rootstocks were removed at the beginning of each growing season. The herbaceous layer and the cryptogam cover were not removed. In order to examine the effect of the trench on soil water content, gravimetric soil moisture determinations were made along 3 equidistant radiating lines from each juvenile. The South radius usually tended upslope. Samples were taken at 50 and 150 cm along each radius for a total of 6 samples per tree. Each soil sample was collected in the 5–15 cm depth soil in July and August 1980.

For age determinations the experimental western hemlocks were too large for terminal bud scars to be counted, yet too small for age determinations via an increment borer. Since the project was designed as a long term study, age determination via harvesting was not possible. Thus, ages of experimental western hemlocks were estimated from a linear regression of height with age calculated using the western hemlocks removed from logs during the root zone manipulation experiment ($r^2 = 0.69$; Fig. 1). The height of each removed western hemlock was recorded, and a cross-section from the base of the bole was collected for age determination by counting annual rings. Since each treatment contained individuals within the range of heights, it was not possible to analyze growth data for an age effect.

Canopy manipulations

Small gaps were created in the canopy by removing *Rhododendron* branches or branches of small trees; intermediate gaps were created by cutting western hemlock or yews < 5 m tall; and one large gap was created by felling two western hemlock trees (DBH = 30.0 cm and 26.5 cm). The amount of light available to each western hemlock juvenile used in the study was measured with Ozalid paper

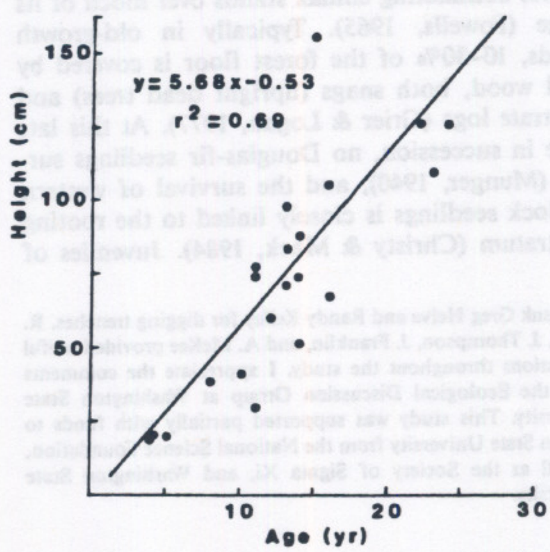

Fig. 1. Linear regression of height (cm) to age (yr) of 24 individuals of *Tsuga heterophylla* from the understory of the old-growth stand.

light meters following Friend (1961) before and after canopy manipulations. A calibration curve was obtained by exposing a series of such petri dish assemblies of Ozalid paper to sunlight for various time intervals at a meteorological station on the H. J. Andrews Experimental Forest. The number of bleached sheets was equated to short-wave radiation in Langleys (ly = gr cal cm^{-2} hr^{-1}) as recorded by a Kipp Solarimeter. Exposures were made at increasing time intervals from 30 min to 24 hr. The calibration and Ozalid meter measurements were conducted simultaneously on clear days.

Measurements

Canopy manipulations are hereafter referred to as 'pruning' and root zone manipulations as 'trenching' for juveniles on either soil or logs. There were 3 treatment categories: Increased light (pruned but not trenched, designated Pr; N = 18); decreased root competition (not pruned but trenched, Tr; N = 24); and both increased light and decreased root competition (both pruned and trenched, PrTr; N = 16). Controls were neither pruned nor trenched (N = 22). The following was recorded for each western hemlock juvenile: Rooting substratum (log or soil), basal diameter; length of entire trunk; length of one vigorous branch; leader (annual) growth of trunk each year; and leader (annual) growth of the same branch each year. Lateral leader and terminal leader refer to the growth for one particular growing season. Measurements were made in the middle of the growing season (July) and at the end of the growing season (November) in 1979 and July 1981.

At the onset of this experiment, the individuals assigned to each treatment were similar with respect to all variables measured except the branch-leader initial length (Table 1). Juveniles in the trenched treatment had significantly longer branch-leaders than the means for the other 3 treatments ($P<0.05$). Analysis of variance (ANOVA) was used to test for growth differences among treatments and the control (Table 1). The Least Significant Difference test (LSD) served to establish significance of differences between means. All statistical tests were performed with the SAS package of computer programs (Helwig & Council, 1979).

Results

Growth of the previously suppressed western hemlocks was increased by minimizing root competition (Tr treatments) and to a lesser degree by altering the canopy (Pr treatment) (Table 2A). The increase in length of both the trunk and one major branch was significantly greater in the trenched groups than in the nontrenched groups (Table 2A). Canopy alteration resulted in no significant difference in growth of either the trunk or the branch length (Table 2A, $P \leq 0.05$).

The combination of the 2 manipulations (PrTr) did now show a strong synergistic effect (Table 2B). Basal diameter of controls increased 0.05 cm while in the 3 treatments plants showed increases of 0.17 and 0.19 cm (Table 2B). Initial basal diameter of trenched plants was significantly greater than the controls (Table 2B, $P<0.05$), but the means for basal diameter growth in trenching and pruning treatments were not significantly greater than means of growth in the controls (Table 2B, $P \leq 0.05$). The terminal leader was the only variable which showed a significant increase in growth in the pruned treatment and trenched treatment over control plants ($P<0.05$) and a highly significant increase in growth due to both pruning and trenching (PrTr, $P \leq 0.025$).

Table 1. Initial means ± standard error (se) of growth measurements for 80 individuals of western hemlock (40 – 200 cm tall) in the old-growth stand used in this study. Differences among means for each variable were nonsignificant, except for lateral leader (ANOVA, df=3, * = $P \leq 0.05$). Initial measurements (cm) were taken in 1979.

Treatment	N	Basal diameter	Trunk length	Terminal leader	Branch length	Lateral leader
Control	22	1.88 ± 0.15	127.6 ± 8.5	7.0 ± 0.7	64.8 ± 4.8	4.9 ± 0.6
Pr	18	1.78 ± 0.17	135.3 ± 9.4	5.1 ± 0.7	61.7 ± 5.3	4.9 ± 0.6
Tr	24	1.64 ± 0.14	123.8 ± 8.1	7.6 ± 0.6	61.7 ± 4.7	6.5 ± 0.5*
Pr Tr	16	1.88 ± 0.18	132.0 ± 9.9	5.5 ± 0.8	64.8 ± 5.6	4.6 ± 0.6

Table 2. Means ± standard error (se) of growth measurement, for 80 individuals of *Tsuga heterophylla* in the understory of the old-growth stand. Growth (cm) of basal diameter, trunk length and branch length was measured as the increase from July 1979 to July 1981. Growth of terminal (= trunk) and lateral (= branch) leaders was defined as the ratio of final leader length (July 1981) divided by the initial leader length (November 1979). For each variable, means followed by a different letter are significantly different; tested by ANOVA and LSD, $df = 1$ for A and $df = 3$ for B. A. Main effects of root zone manipulation (= trenching) and canopy manipulation (= pruning). B. Three treatments comparing growth to the Control.

Treatment	*N*	Basal diameter (cm)	Trunk length (cm)	Terminal leader ratio	Branch length (cm)	Lateral leader ratio
A.						
Trenching:						
Trenched	40	0.18 ± 0.04	16.6 ± 1.5a	1.5 ± 0.1a	14.5 ± 1.0a	1.4 ± 1.4
Not trenched	40	0.12 ± 0.04[1]	11.1 ± 1.4b[3]	1.1 ± 0.1b[2]	9.4 ± 1.0b[4]	3.1 ± 1.4[1]
Pruning:						
Pruned	34	0.18 ± 0.04	14.5 ± 1.6	1.6 ± 0.1a	12.8 ± 1.1	1.7 ± 1.5
Not pruned	46	0.12 ± 0.03[1]	13.2 ± 1.3[1]	1.0 ± 0.1b[4]	11.1 ± 0.9[1]	2.8 ± 1.3[1]
B.						
Control	22	0.05 ± 0.05a	11.5 ± 1.9a	0.9 ± 0.1a	9.2 ± 1.4a	4.6 ± 1.9
Pr	18	0.18 ± 0.05ab	10.7 ± 2.1a	1.4 ± 0.2b	9.6 ± 1.5a	1.7 ± 2.1
Tr	24	0.19 ± 0.05b	15.0 ± 1.9ab	1.1 ± 0.1b	13.0 ± 1.3b	1.1 ± 1.8
PrTr	16	0.17 ± 0.06ab[2]	18.3 ± 2.3b[2]	1.8 ± 0.2c[2]	15.9 ± 1.6b[2]	1.7 ± 2.2[1]

[1] NS; [2] $P < 0.05$; [3] $P < 0.01$; [4] $P < 0.001$.

Each of the treatments and the control was subdivided into the 2 rooting substrata (soil or log). The decay classes of the logs (Triska & Cromack, 1979; Sollins, 1982) included classes 3, 4 and 5 (moderate to extreme decomposition), but no attempt was made to compare growth differences of western hemlock rooted on particular decay classes of logs. Seedling recruitment and survival of western hemlock is closely linked to decay classes (Christy & Mack, 1984). When the means for any

Table 3. Growth ± standard error (se) of suppressed individuals of *Tsuga heterophylla* subdividing each treatment on the basis of rooting substratum (log or soil). Growth expressed as in Table 2. For each variable, means followed by a different letter are significantly different; ns = nonsignificant difference; tested by ANOVA and LSD, df = 1 for A and df = 7 for B. A. $\bar{x} \pm$ se of growth for main effect of rooting substratum. B. $\bar{x} \pm$ se of growth for treatments and control subdivided on the basis of rooting substratum.

Treatment	*N*	Basal diameter (cm)	Trunk length (cm)	Terminal leader ratio	Branch length (cm)	Lateral leader ratio
A.						
Rooting substratum:						
Soil	45	0.14 ± 0.03	14.6 ± 1.4	1.3 ± 0.1	11.1 ± 0.9	1.4 ± 1.3
Log	35	0.16 ± 0.04[1]	12.5 ± 1.6[1]	1.2 ± 0.1[1]	13.5 ± 1.1[1]	3.0 ± 1.6[1]
B.						
Control-soil	10	0.09 ± 0.07a	10.4 ± 2.9a	0.9 ± 0.2a	7.6 ± 2.0a	0.8 ± 2.8
Control-log	12	0.02 ± 0.07ab	12.3 ± 2.6ab	0.9 ± 0.2a	10.6 ± 1.8ac	7.7 ± 2.6
Pr-soil	11	0.13 ± 0.07ab	12.6 ± 2.8ac	1.5 ± 0.2bc	9.4 ± 1.9ac	2.1 ± 2.7
Pr-log	7	0.27 ± 0.09b	7.9 ± 3.5a	1.2 ± 0.2ac	10.0 ± 2.3ac	1.1 ± 3.4
Tr-soil	13	0.18 ± 0.06ab	16.6 ± 2.5ac	1.2 ± 0.2a	14.1 ± 1.7ac	1.0 ± 2.5
Tr-log	11	0.19 ± 0.07ab	13.0 ± 2.8ac	0.9 ± 0.2a	11.6 ± 1.9ac	1.3 ± 2.7
PrTr-soil	11	0.17 ± 0.07ab	18.8 ± 2.8bc	1.8 ± 0.2b	13.4 ± 1.9c	1.7 ± 2.7
PrTr-log	5	0.16 ± 0.10ab[2]	17.0 ± 4.1ac[2]	1.9 ± 0.3b[2]	21.6 ± 2.8b[2]	1.7 ± 4.0[1]

[1] NS; [2] $P < 0.05$.

Table 4. Amount of light (Langleys) available to suppressed individuals of *Tsuga heterophylla* in the old-growth stand used in this study. Measurements were taken before canopy alteration in September 1979 and after canopy alteration in August 1980. Increase in light (ly) = $\bar{x}$ after alteration − $\bar{x}$ before alteration. Rated increase was obtained by setting the lower of the means for treatments without canopy manipulation (Tr) to zero and adjusting each of the means by subtracting that lower value.

Treatment	N	Before $\bar{x} \pm$ sd	After $\bar{x} \pm$ sd	Increase in light	Rated increase
Control	21	4.1 ± 2.2	40.2 ± 16.0	35.7 ± 15.4	+ 4.2
Pr	18	2.5 ± 1.6	47.6 ± 27.6	45.2 ± 28.2	+ 13.7
Tr	24	5.7 ± 3.8	35.8 ± 14.6	31.5 ± 11.2	0
PrTr	16	5.0 ± 4.4	52.7 ± 25.5	47.6 ± 26.0	+ 16.2

variable of individuals rooted in soil were compared to those rooted on logs, the differences were nonsignificant (Table 3A; $P \leq 0.05$). With the exception of lateral length in the pruned and trenched treatment, the means for each variable were not significantly different within a treatment (Table 3B, $P \leq 0.05$). Thus changes in growth can be attributed to either trenching or canopy alteration.

The Ozalid paper meters allowed an estimation of increased light (lumination, in Langleys) available to each western hemlock after the alteration of the canopy. The Ozalid booklets used with each of the 80 juveniles were analyzed separately, and the number of sheets exposed was determined. Calibration curves were used to equate exposed sheets to amount of light available to each western hemlock. Ideally, the 2 treatments which included no canopy manipulations (control and Tr) would show no change in light levels. The value for the trenching treatment was used as a reference. A rated increase was obtained by setting the lower of the means for treatments without canopy manipulations (Tr) to zero and adjusting each of the means by subtracting that lower value (Table 4). Juveniles in the 2 treatments with canopy manipulation experienced increased light: pruning (Pr) = +13.7 ly or an increase of 30% above reference lumination; and pruning and trenching (PrTr) = +16.2 ly or an increase of 34% above reference lumination.

The plastic lining around each trench had no significant effect on water content in the soil, inside (50 cm) or outside (150 cm) the trench ($P \leq 0.05$), downslope (NW and NE) or upslope (S). Mean moisture content, based on soil dry weight, ranged between 55% and 72% (Table 5).

A total of 24 age determinations were made from basal disks of western hemlock juveniles removed during the trenching and pruning manipulations in the summer of 1979 (Fig. 1). The correlation of height (cm) to age (yr as determined by counting xylem rings) was satisfied by the equation: $y = 5.58 \times -0.53$ ($r^2 = 0.69$). Using this equation, the ages of western hemlock juveniles used in the manipulation experiments were estimated to be less than 35 years old. Each treatment category included juveniles in the entire range of height (40–200 cm); therefore, height (or age) cannot be taken into account in the analysis of treatment effects.

Table 5. Soil moisture content (percent ± se) in the old-growth forest used in this study in July 1980. A. Samples were taken inside a trench (50 cm from base of hemlock) and outside trench (150 cm from base of hemlock). $N = 15$ for each distance along each radius (3 directions around base of trunk × 5 trees per treatment). Tested with ANOVA, df = 3, all results nonsignificant. B. Samples were taken downslope (NE and NW) and upslope (S) from the hemlock at a distance = 50 cm along each radius. Similar means were found when tested at 150 cm along each radius. $N = 5$. Tested with ANOVA, df = 3, all results nonsignificant.

A. Distance away from western hemlock

Treatments	50 cm	150 cm
Tr	60.21 ± 15.5	62.63 ± 9.2
PrTr	58.04 ± 13.8	65.78 ± 6.5

B. Direction

Treatments	NE	NW	S
Control	70.48 ± 4.0	65.04 ± 14.0	72.4 ± 5.9
Pr	66.60 ± 4.4	67.54 ± 7.7	58.9 ± 12.8
Tr	55.82 ± 19.4	62.79 ± 18.1	62.0 ± 10.1
PrTr	59.87 ± 14.7	55.23 ± 17.7	59.0 ± 11.1

Discussion

Effects of competition are difficult to demonstrate unambiguously (Harper, 1977), however, the data presented here suggest an interaction exists between the suppressed individual western hemlocks in the forest understory and neighboring plants. Root competition had the stronger influence in suppressing growth, as suggested by release in growth following root zone manipulation. The manipulations in these experiments have natural analogs in old-growth forests. The light levels for western hemlock juveniles are altered when a gap is created in the canopy without disturbing belowground activity. Such canopy disturbance occurs when the crown of a nearby overstory tree is removed or when a standing dead tree is partially snapped off in a storm. Release from belowground competition occurs when a neighboring tree(s) is blown over (wind-thrown) or dies and remains standing (snag). Thus both a wind-thrown tree and a snag would alter the resources available to a suppressed western hemlock within its biological space (*sensu* Ross & Harper, 1972).

The presence of the plastic-lined trenches did not result in increased soil moisture inside the trenched area, as an earlier study of trenches without linings reported (Toumey & Kienholz, 1931). Consequently, soil moisture was not considered to be a limiting resource, since the western hemlocks rooted in soil in different treatments had similar amounts of available moisture and yet showed different growth responses.

Although new roots were not invading the trenched area, the trenches did not eliminate entirely root competition since the severed rootstocks of *Rhododendron*, *Acer circinatum*, and *Berberis* resprouted within the area enclosed by the trench in the following growing season. For juveniles on logs new roots may have invaded the trenched area, or the juvenile's roots may have grown past the trenched zone. In either case, the root zone manipulation greatly decreased the amount of belowground competition. Unfortunately, it is not possible to quantify the amount of change belowground as it was for the aboveground change.

Western hemlock is unusual among conifers in the low elevation coastal forests in the Pacific Northwest in preferentially establishing as an understory species on partly decayed, large-diameter logs on the forest floor (Minore, 1972; Franklin *et al.*, 1981; Christy & Mack, 1984). The two substrata included in this study provide quite different nutrient availabilities (Sollins, 1982), however, initial growth response was not influenced by the substratum. Perhaps over a longer time the character of the rooting substratum may affect growth, but in the initial response to release, there was no significant difference in response of juveniles rooted on logs versus soil.

The aboveground resources did not appear to be limiting since growth was not stimulated by increased light availability to the suppressed western hemlocks. Zeide (1980) reported that Eastern European forest tree species are more sensitive to light limitations than to deficiencies in heat, soil moisture and soil fertility. Ozalid paper, by being sensitive to only the lower end of visible light (blue light), presents one limitation in measuring the alteration of light levels. The technique is appropriate, however, as an index of canopy alteration since the spectral distribution of light beneath a mixed coniferous canopy (*Pseudotsuga menziesii, Abies concolor,* and *Pinus ponderosa*) contains a larger proportion of blue light (400–450 nm) (Jarvis *et al.*, 1976) and somewhat more red light (650–700 nm) (Atzet & Waring, 1970) than found beneath broadleaved canopies. The responses of the seedlings of conifers to various light quality regimes has not been studied, however, it seems likely that a shade tolerant species such as western hemlock would be adapted to respond to the spectral changes and low light levels typical in mature and old-growth stands.

Changes in the canopy structure have been reported as an enhancement to establishment of *Pinus taeda* (Peet & Christensen, 1980), *Pinus contorta* (Whipple & Dix, 1979), and *Cryosophila guagara*, a tropical palm (Richards & Williamson, 1975). Canopy gaps have been correlated also to rapid growth of coniferous and deciduous trees in the understory of old-growth forests (Lorimer, 1980). Canopy manipulation in this study produced approximately a 30–34% increase in the overall amount of light available to the suppressed western hemlocks. But overall light is not a true picture of light availability since sunflecks may be an important source of incoming radiation to understory conifers under multilayered canopies. However, such transient light cannot be measured alone with the technique used here. Hodges (1967) found that under a dense Douglas-fir stand, net photosynthesis was primarily dependent on occasional sunflecks. Light response for western hemlock is unknown; creating gaps in the canopy may be important to the suppressed juveniles only if an increase in light leads to an increase in net photosynthesis which then translates to increased growth.

An extended experimental time frame in which western hemlock may respond to the manipulations of both aboveground and belowground resources is necessary to follow changes in growth. The correlation between height and age in woody perennials is generally poor (Harper, 1977), especially for suppressed trees. The height:age correlation provides an estimation that the western hemlocks in this study (40–200 cm tall) were less than 35-years-old. The timing of removal of competition is important for some herbaceous species as individuals may not overcome initial disadvantages caused by competition (Haizel & Harper, 1973). Results so far with western hemlock do not reveal an age at which release from competition does not cause increased growth. Meyer (1937) reported 50-year-old suppressed western hemlocks developed into a vigorous stand when the overstory was removed. In this study, all experimental juveniles responded to alterations of the environment.

This study presents initial results of release from aboveground and belowground limiting factors of a coniferous species in a naturally occurring forest community. The effects of altering the root environment are greater than the effects resulting from alteration of the canopy. Growth of individual trees into the overstory canopy certainly is a function of the death of overstory members of the community with accompanying release of resources (Franklin *et al.*, 1981). The population may be regulated in this manner, with a 1:1 replacement of old trees occurring over long time periods. Frequency of those events – wind-throws, lightning fire in the canopy, fungal or insect attack – that open gaps in the canopy or kill an adult tree, could then govern patterns of tree recruitment from the bank of persistent seedlings into the overstory.

References

Atzet, T. & Waring, R. H., 1970. Selective filtering of light by coniferous forests and minimum light energy requirements for regeneration. Can. J. Bot. 48: 2163–2167.

Christy, E. J. & Mack, R. N., 1984. Variation in demography of juvenile Tsuga heterophylla across the substratum mosaic. J. Ecol. 72: 75–91.

Eis, S., 1974. Root system morphology of western hemlock, western red cedar, and Douglas fir. Can. J. Forest Res. 4: 28–38.

Fowells, H. A., 1965. Silvics of forest trees of the United States. USDA Forest Serv. Agric. Handbook No. 271, 762 pp.

Franklin, J. F., Cromack, Jr. K., Denison, W., McKee, A., Maser, C., Sedell, J., Swanson, R. & Juday, G., 1981. Ecological characteristics of old-growth Douglas fir forests. USDA Forest Serv. Gen. Tech. Rep. PNW-118, 48 pp.

Franklin, J. F. & Hemstrom, M. A., 1981. Aspects of succession in the coniferous forests of the Pacific Northwest. Forest Succession. In: D. C. West, H. H. Shugart & D. B. Bodkin (eds.), pp. 212–229, Springer, New York.

Friend, D. T. C., 1961. A simple method of measuring integrated light values in the field. Ecology 42: 577–580.

Grier, C. C. & Logan, R. S., 1977. Old-growth *Pseudotsuga menziesii* communities of a western Oregon watershed: biomass distribution and production budgets. Ecol. Monogr. 47: 373–400.

Grime, J. P., 1979. Plant Strategies and Vegetation Processess. John Wiley & Sons. London. 222 pp.

Haizel, K. A. & Harper, J. L., 1973. The effects of density and the timing of removal on interference between barley, white mustard, and wild oats. J. Ecol. 61: 23–31.

Harper, J. L., 1977. Population Biology of Plants. Academic Press. New York. 892 pp.

Hawk, G. M., Franklin, J. F., McKee, W. A. & Brown, R. B., 1978. H. J. Andrews Experimental Forest reference stand system: establishment and use history. US/IBP Coniferous Biome Bull. No. 12. Coll. Forest Res. Univ. of Washington, Seattle, 79 pp.

Helwig, J. T. & Council, K. A., 1979. SAS User's Guide, 1979 Edition. SAS Institute Inc., Cary, N.C. 494 pp.

Hodges, J. D., 1967. Patterns of photosynthesis under natural environmental conditions. Ecology 48: 234–242.

Jarvis, P. G., James, G. B. & Landberg, J. J., 1976. Coniferous forest. In J. L. Monteith (ed.), Vegetation and the Atmosphere. V. 2. Case Studies. pp. 171–240. Academic Press, New York.

Lorimer, C. G., 1980. Age structure and disturbance history of a southern Appalachian virgin forest. Ecology 61: 1169–1184.

Meyer, W. H., 1937. Yield of even-aged stands of Sitka spruce and western hemlock. USDA Forest Serv. Tech. Bull. 544. 83 pp.

Minore, D., 1972. Germination and early growth of coastal tree species on organic seed beds. USDA Forest Serv. Res. Pap. PNW-135. 18 pp.

Munger, T. T., 1940. The cycle from Douglas fir to hemlock. Ecology 21: 451–459.

Peet, R. K. & Christensen, N. L., 1980. Succession: A population process. Vegetatio 43: 131–140.

Richards, P. & Williamson, G. B., 1975. Treefalls and patterns of understory species in a wet lowland tropical forest. Ecology 56: 1226–1229.

Ross, M. A. & Harper, J. L., 1972. Occupation of biological space during seedling establishment. J. Ecol. 60: 77–88.

Santantonio, D., Herman, R. K. & Overton, W. S., 1977. Root biomass studies in forest ecosystems. Pedobiologia, BD 175: 1–31.

Sollins, P., 1982. Input and decay of coarse woody debris in

coniferous stands in Oregon and Washington. Can. J. Forest Res. 12: 18–28.
Triska, F. J. & Cromack, Jr. K., 1979. The role of wood debris in forests and streams. In: R. H. Waring (ed.), Forests: Fresh perspectives from ecosystem analysis. pp. 171–190. Proc. 40th Ann. Bio. Coll., Oregon State Univ. Press.
Toumey, J. W. & Kienholz, R., 1931. Trenched plots under forest canopies. Yale Univ. School For. Bull. 30: 1–31.
Waring, R. H., Holbo, H. R., Bueb, R. P., & Fredriksen, R. L., 1978. Documentation of meteorological data from the coniferous forest biome primary station in Oregon. USDA Forest Serv. Gen. Tech. Rep. PNW-73, 23 pp.
Whipple, S. A. & Dix, R. L., 1979. Age structure and successional dynamics of a Colorado subalpine forest. Am. Mid. Nat. 101: 142–158.
Zeide, B., 1980. Ranking of forest growth factors. Env. Exp. Bot. 20: 421–427.

Accepted 26.6.1985