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VARIATION IN DEMOGRAPHY OF JUVENILE *TSUGA HETEROPHYLLA* ACROSS THE SUBSTRATUM MOSAIC

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SUMMARY

(1) Recruitment and survival of juvenile *Tsuga heterophylla* were followed on different substrata on the west slope of the Cascade Range, central Oregon, U.S.A.

(2) Whilst seeds fell mainly from October to March, some were shed in all but six of thirty-two consecutive months.

(3) Almost all juveniles occurred on decaying logs even though fallen timber may cover only 10–30% of the forest floor.

(4) Recruitment on all substrata varied widely from year to year, as expected in a conifer with mast years of seed production.

(5) Cohorts emergent in different months during one calendar year often showed greatly different survivorship curves even on the same rooting substratum.

(6) Mortality was much higher for juveniles during the first 2 yr after emergence than in subsequent years. Microtine rodents probably account for most seed and seedling deaths.

(7) The extent of decay of woody rooting-substrata does not influence percentage emergence, although survival of juveniles was most prolonged on *Pseudotsuga menziesii* logs with rotten heartwood.

(8) The age-class structures of juvenile populations were functions of the fraction of the forest floor covered by fallen wood in each decay class.

INTRODUCTION

Soil surfaces are very heterogeneous and provide a mosaic of sites for seed lodgement and germination. As a result, recruitment and subsequent survival of seedlings may differ substantially with change in the availability of microsites (Harper, Williams & Sagar 1965; Law 1981). In forests, tree-fall is a major source of such heterogeneity by creating gaps in an otherwise continuous light-limiting canopy (Hartshorn 1978; Whitmore 1982). Seedlings with high light compensation points may be restricted to new gaps. Tree-fall also creates variation in the micro-environment relevant to recruitment by providing logs which decay and may become colonized (Thompson 1980). This consequence of the death of an adult tree is often overlooked, yet it is particularly important in the low-altitude forests along the Pacific coast and west slope of the Cascade Range in western North America. In these coniferous forests, the regeneration of *Tsuga heterophylla*† is mainly on stumps and prostrate logs (Fowells 1965).

Tsuga heterophylla (western hemlock) occurs along the Pacific coast from the Kenai Peninsula in Alaska to north-western California and in the mountains of north-eastern Washington, northern Idaho, north-western Montana and south-eastern British Columbia (Fowells 1965). It has high tolerance of shade (Minore 1972) and of competition in even-aged stands. Some seeds are produced every year, whilst mast years occur every 3–4

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† Nomenclature follows Hitchcock & Cronquist (1973) for vascular plants, Lawton (1971) for mosses, and Clark & Frye (1928) for liverworts.

yr. Stand maintenance is dependent exclusively on this seed production as *T. heterophylla* does not propagate from roots or stumps (Fowells 1965). *Tsuga heterophylla* is unusual among western North American conifers in dominating an eventual climax community throughout most of its range (Fowells 1965; Franklin & Hemstrom 1981). On the western slopes of the Cascade Range, *T. heterophylla* succeeds seral *Picea sitchensis* and *Pseudotsuga menziesii* (Franklin & Dyrness 1973 and is an important source of softwood (Beswick 1976).

The widely observed restriction of juveniles of *Tsuga heterophylla* to 'nurse logs' (Franklin & Dyrness 1973) suggested that its recruitment and survival might be dependent on the changing availability of various substrata, including logs of various species in various states of decay. Juveniles are defined here as individuals more than 4 m tall and less than 35 yr old.

STUDY AREA

The study was conducted within advanced seral or old-growth stands (*sensu* Franklin & Hemstrom 1981), between sea level and 1000 m altitude on the west slope of the Cascade Range (Franklin & Dyrness 1973). *Pseudotsuga menziesii* commonly dominates these stands along with *Tsuga heterophylla* and individuals of both species may reach to 250–550 years old. A large volume of dead wood (both snags (branch remains) and prostrate logs) covers 10–30% of the forest floor and comprises 1–3 kg m^{-2} of organic matter (Grier & Logan 1977; Franklin & Waring 1980). Cryptogams, which form a conspicuous layer on the soil surface throughout the stands, include mosses such as *Eurhynchium oreganum*, *Hylocomium splendens* and *Rhytidiadelphus triquetrus* and liverworts such as *Scapania bolaneri*. Annual precipitation averages 2400 mm, of which 70% falls between November and March. Summers are mostly dry (Waring *et al.* 1978).

Most of the study was conducted in such an advanced seral stand in the *Tsuga heterophylla/Rhododendron macrophyllum/Berberis nervosa* habitat type (Hawk *et al.* 1978) along Lookout Creek (44°13′33″N, 122°13′8″W; 512 m altitude) in the H. J. Andrews Experimental Forest (6075 ha), Lane Co., Oregon. The order of overstory dominance (based on basal area) in the stand was: *Tsuga heterophylla* > *Pseudotsuga menziesii* > *Thuja plicata*. Detailed community descriptions have been prepared from several permanent plots (reference stands) in the same habitat type within the Experimental Forest (Hawk *et al.* 1978). For convenience *Tsuga heterophylla*, *Pseudotsuga menziesii* and *Thuja plicata* will be referred to subsequently by their generic names only.

METHODS

Occurrence of juveniles on woody substrata

Distribution of the juveniles among the various substrata was examined initially in Reference Stand 7 (0·25 ha) in the *Tsuga/Polystichum munitum/Oxalis oregana* habitat type. The dominance hierarchy (reflected in basal area) in this stand is: *Pseudotsuga* > *Tsuga* > *Thuja* (altitude 520 m; NW aspect, see Hawk *et al.* 1978 for other stand characteristics). Twenty-five 1 × 2 m plots were arranged at 1-m intervals along each of two parallel northerly and two parallel westerly transects (total area sampled 200 m²). The transects intersected at the 10 m and 40 m points along each line. The rooting substratum of all individuals of *Tsuga heterophylla* less than 1 m tall was recorded and included decaying logs and litter surfaces without visible woody fragments.

Seed rain measurement

Falling seeds of *Tsuga*, *Pseudotsuga*, *Thuja* and *Taxus brevifolia* were collected in twenty-four circular litterfall traps (22 cm diameter) placed at random within a 100 × 100 m plot in Reference Stand 2 (see Hawk *et al.* 1978 for stand characteristics), approximately 3 km from the Lookout Creek study site. Traps were emptied monthly.

Census of the population on logs

Census of juveniles of *Tsuga* (<4 m tall) began in July 1979 with the demarcation of all dead and fallen logs intercepted along a 100-m westerly transect in the Lookout Creek study site. On these logs all juveniles with diameters greater than 3 mm were tagged for future identification with vinyl plastic material tied around the stems. Seedlings less than 3 mm diameter were tagged by placing plastic flagging on sewing pins inserted into the log beside them. Additional recruitment and any deaths were detected in similar censuses conducted at least every 2 months from September 1979 to September 1981. Precise age determinations could be made for the five previous years of growth by counting terminal bud scars. Seedlings more than 5 yr old were grouped into a pre-1975 age-class. For individuals which emerged after September 1979 the emergence date is known to within 60 days. All tagged individuals were assigned to a cohort, which is defined here as all individuals emerging between two censuses.

Twenty-six fallen logs, identified to species, were included in the study. Structural characteristics of a fallen log depend on its species and amount of decomposition (Table 1). The total length, cross-sectional area and decay class at each end of the trunk, and overall decay class for the trunk were determined. From these data, a projected area of each log was calculated (Table 2). Five of the twenty-six logs had been wind-thrown and juveniles occurring on the mounds of soil covering the root systems of these boles were also included in the study. The percentage of the forest floor covered by logs in each decay class was determined in the stand in four 25 × 25 m plots along or near the transect. The areal extent of each log was calculated from measurements of log length and average width. The extent of the mounds was not determined.

TABLE 1. Decay classification used in this study for fallen logs of *Pseudotsuga menziesii* and *Thuja plicata* in forests of Western Oregon. Characteristics of the decay classification which are based on Graham (1981) and Sollins (1982) are indicated with * and †, respectively.

Characteristic	1	2	3	4	5
			Decay class		
Percentage of log surface still covered by bark*	100	80–99	40–79	10–40	0–9
Structural integrity*	Sound throughout	Sapwood somewhat decayed; heartwood sound	Sapwood rotted–sloughing; heartwood mostly sound	Sapwood sloughing–missing; heartwood 80% rotted	None: Sapwood missing: heartwood cubical, sloughing
Log capable of supporting its own weight†	Yes	Yes	Yes	No	No
Extent of log's branch system†	Small twigs attached	Only larger twigs with entire branch system	Only large branches attached (length > diameter of log)	Only branch stubs present or none (length < diameter of log)	No discernible branch stubs
Distribution of invading roots†	Absent	Restricted to the trunk surface; ephemeral	Sapwood only	Throughout	Throughout
Rooted vegetation†	None	No seedlings > 1 yr old	*Tsuga* < 2 m tall; few shrubs; cryptogams present	*Tsuga* < 15 cm dbh: shrubs < 2 m tall; cryptogam cover complete	*Tsuga* up to 200 cm dbh, shrubs > 2 m tall; cryptogam cover complete

TABLE 2. Total number of juveniles of *Tsuga heterophylla* within annual cohorts that were rooted before July 1979 and September 1981 on each of six substrata along a 100-m transect in a forest in Oregon, U.S.A. Numbers of individuals in the 1979 and 1981 cohorts found on each substratum were compared with a χ^2 test. The expected number for that substratum is given in parentheses. Expected number = (substratum area/total substratum area) (total number in annual cohort); df = 1 in all cases. Symbols: *, $P < 0.05$; **, $P < 0.0001$.

| | | | | Cohorts | | | | | Woody debris | |
Substratum	pre-1975	1975 and 1976	1977 and 1978	1979	1980	1981	Total present	Total surviving until September 1981	Projected area of substrata included in the census, m²	Percentage surface area covered by woody debris in the stand
Pseudotsuga logs decay class 3	434	192	233	802** (928) $\chi^2 = 17\cdot1$	16	1536** (1862) $\chi^2 = 57\cdot1$	3213	1138	226	3·2
Pseudotsuga logs decay class 4	376	137	171	779** (405) $\chi^2 = 345$	17	1302** (813) $\chi^2 = 294$	2782	1344	98·8	2·6
Pseudotsuga logs decay class 5	8	0	1	15** (63) $\chi^2 = 36\cdot5$	15	95* (127) $\chi^2 = 8\cdot06$	120	9	15·4	1·1
Thuja logs decay class 3	44	4	60	46** (159) $\chi^2 = 80\cdot3$	6	503** (319) $\chi^2 = 106$	663	218	38·8	1·6
Tsuga logs decay class 5	0	0	0	0* (5) $\chi^2 = 5$	0	19** (11) $\chi^2 = 5\cdot82$	19	0	1·4	·3
Mounds	116	9	21	166** (248) $\chi^2 = 27\cdot1$	3	174** (497) $\chi^2 = 209$	489	201	60·3	—
Totals	978	342	486	1808	43	3629	7286	2910	441	9·2

Demography of Tsuga heterophylla

An initial census of any juveniles on non-woody substrata also was attempted in July 1979 in six 1 × 25 m strips located at random within the stand. No juveniles were found and the strips were abandoned.

Recruitment and survival of seedlings derived from sown seeds

In autumn 1979, seeds of *Tsuga* were collected by the U.S. Forest Service in the *Tsuga heterophylla* zone (Franklin & Dyrness 1973) at 450–600 m altitude, approximately 30 km south of the study site, and stored at 4 °C. In June 1980, lots, each of fifty seeds from this collection, were sown onto each of the following nine substrata (treatments) in 2 × 5 dm plots within the study site: exposed mineral soil; litter, cryptogams and herbaceous piants; litter and cryptogams; *Pseudotsuga* logs (decay class 3) with cryptogams removed; *Pseudotsuga* logs (decay class 3) with cryptogams left; *Pseudotsuga* logs (decay class 4) with cryptogams left; *Pseudotsuga* logs (decay class 5) with cryptogams left; *Thuja* logs (decay class 3) with cryptogams removed; and *Thuja* logs (decay class 3) with cryptogams left. Logs in decay classes 4 and 5 are rarely found in old-growth forests without a nearly complete cryptogam cover, so these substrata were not paired with plots in which the cryptogams were removed.

Three replicates of each treatment were sown at each of three locations within 50 m of each other. A tenth treatment to examine the extent of seed predation required covering an additional plot of each of the nine substrata at each location with 5 × 5 mm wire mesh (20 × 40 × 24 cm tall). In March 1981 an unseeded plot was established near each of the nine sets of replicates at each of the three locations to measure the fate of seedlings emergent from the unrestricted seed rain. Percentage emergence data were pooled from the three locations and were analysed using a 2 × 9 factorial analysis of variance and least significant difference on the arcsin transformed data. Tests for significant differences were performed among all treatments.

RESULTS

Occurrence of juveniles on woody substrata

Preliminary evidence of the higher occurrence of the juveniles of *Tsuga* on decaying logs was obtained in Reference Stand 7. Whilst only about 6% of the forest floor in the stand is covered with logs, 247 of 252 juveniles of *Tsuga* in the 200-m^2 area sampled were rooted on logs. Assuming even an approximately uniform seed rain throughout the stand onto all substrata, these results indicate significantly greater occurrence of juveniles ($\chi^2 = 3556$, d.f. = 1; $P < 0.005$) on logs than on other substrata.

Seed rain

Within these old-growth stands, *Tsuga* is a prolific seed producer. Seeds of *Tsuga* comprised about 84% of the seed rain measured by litterfall traps (Fig. 1) in Reference Stand 2 despite only 50% canopy cover for individuals of 1 cm or more dbh in the stand (Hawk *et al.* 1978). *Pseudotsuga*, with a similar canopy cover but less basal area, contributed only 16% of the seed rain. Whilst most *Tsuga* seeds fell in October to March, some seeds of *Tsuga* were recovered in all months except: November 1979; February, August, September and December 1980; and April 1981.

Recruitment

A total of 7286 juveniles, of which 5480 emerged during the period of frequent census from July 1979 to September 1981, was monitored for 27 months; 6797 juveniles were
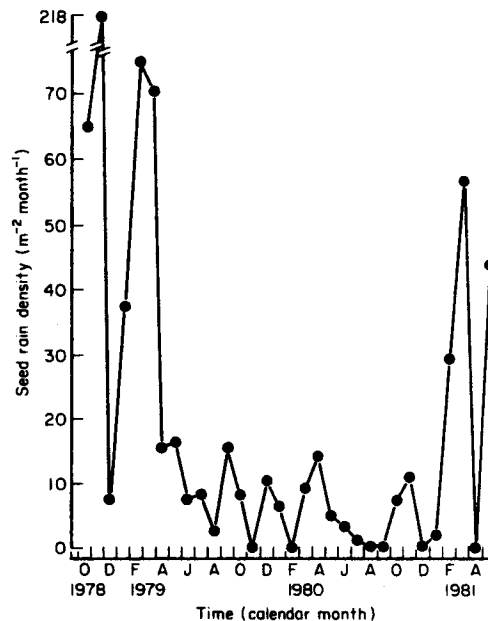
Demography of Tsuga heterophylla

FIG. 1. Seed rain density (numbers falling m^{-2} $month^{-1}$) of *Tsuga heterophylla* in an Oregon forest from October 1978 to May 1981 determined from collections in twenty-four randomly placed litterfall samplers.

rooted on logs, the remainder occurred on mounds. The three cohorts emergent before summer 1979 contributed 1806 juveniles to the total.

The size and time of recruitment differed greatly from year to year and among substrata during the study. Total recruitment of *Tsuga* in 1980 on the 441 m^2 of substrata monitored was low (forty-three seedlings), especially compared with the pre-1975 cohort (978 juveniles), which had survived a minimum of 5 years (Table 2). Whereas only sixteen individuals of *Tsuga* emerged in 1980, 1563 seedlings emerged in 1981 on the same *Pseudotsuga* logs of decay class 3 (Table 2). Figure 2 shows changes in the total population number, in numbers of *Tsuga* newly recruited and in numbers found dead or missing on each census date on *Pseudotsuga* logs of decay class 3. Patterns for logs of decay classes 4 and 5, for *Thuja* logs of decay class 3 and on mounds were broadly similar. In 1980 recruitment of *Tsuga* on *Pseudotsuga* logs of decay class 4 was restricted to March yet on the same substratum in 1981, recruitment occurred from March to July. In 1981, emergence also began in March on *Pseudotsuga* logs of decay class 4 and *Thuja* logs of decay class 3 but was delayed until April on the less decomposed *Pseudotsuga* logs of decay class 3, and mounds. The virtual absence of recruitment during the latter half of 1979 plus 1980 corresponds with the pronounced decline in seed cast in these old-growth stands in this period (Fig. 1). Most emergence in any year probably results from seeds shed less than 6 months earlier.

The relative likelihood of recruitment also differed among substrata. *Pseudotsuga* logs of decay class 4 comprised about 22% of the total woody or mound surfaces along the transect, yet these logs supported a significantly higher number of juveniles from both the 1979 and 1981 cohorts than would be predicted assuming equal opportunity for recruitment among these substrata (e.g., for 1979 data; $\chi^2 = 345$, d.f. $= 1$; $P < 0.0001$). In
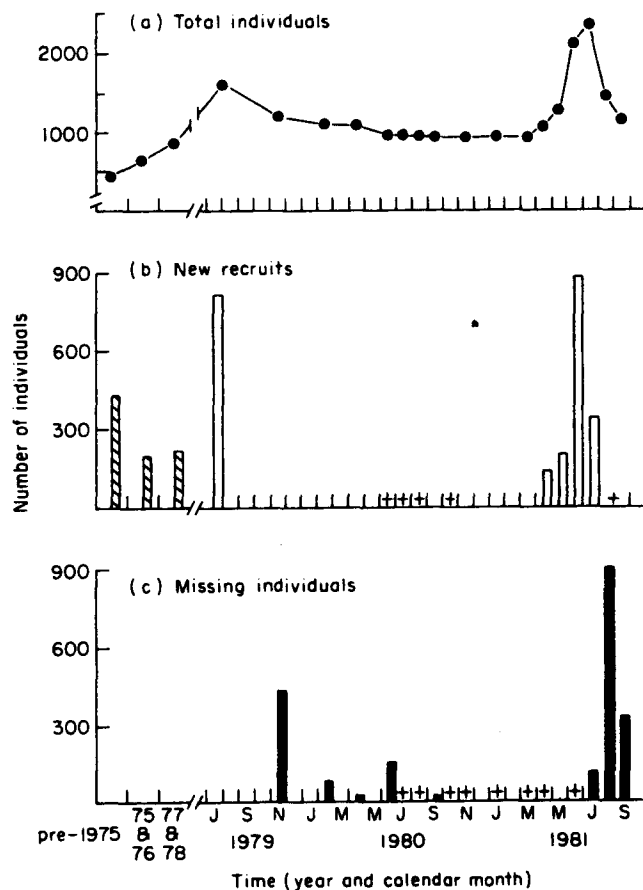
FIG. 2. Recruitment and death of juveniles of *Tsuga heterophylla* in an Oregon forest on *Pseudotsuga* logs of decay class 3. (a) Total number of individuals detected during each census from July 1979 until September 1981, including those juveniles which had emerged prior to July 1979; (b) number of individuals first detected as recruits and (c) first detected missing or dead on each census date. + represents less than ten individuals in a census. Hatched bars represent the number of juveniles which had germinated in three older cohorts of pre-1975, 1975 & 1976, and 1977 & 1978.

contrast, lower numbers of individuals than predicted emerged in both these years on *Pseudotsuga* logs of decay class 3 and mounds (for 1979 data; $\chi^2 = 17 \cdot 1$ and $\chi^2 = 27 \cdot 1$, respectively, d.f. = 1; $P < 0 \cdot 0001$) as well as *Pseudotsuga* logs of decay class 5 (for 1979 data; $\chi^2 = 36 \cdot 5$, d.f. = 1; $P < 0 \cdot 05$). For individuals on other substrata included in the census, results differed little between the 2 years (Table 2).

Survivorship

The total number of *Tsuga* individuals on each substratum increased until autumn 1979 as recruitment continued without any death in the cohorts (e.g. Fig. 2a). Beginning in autumn 1979, mortality reduced the populations. Figure 3 shows survivorship curves for *Tsuga* juveniles. The number of individuals on *Pseudotsuga* logs of decay class 3 and on mounds declined by 25–30% from July to November 1979. A sharp increase in the death rate began in July 1981, mainly among those seedlings which had emerged within the
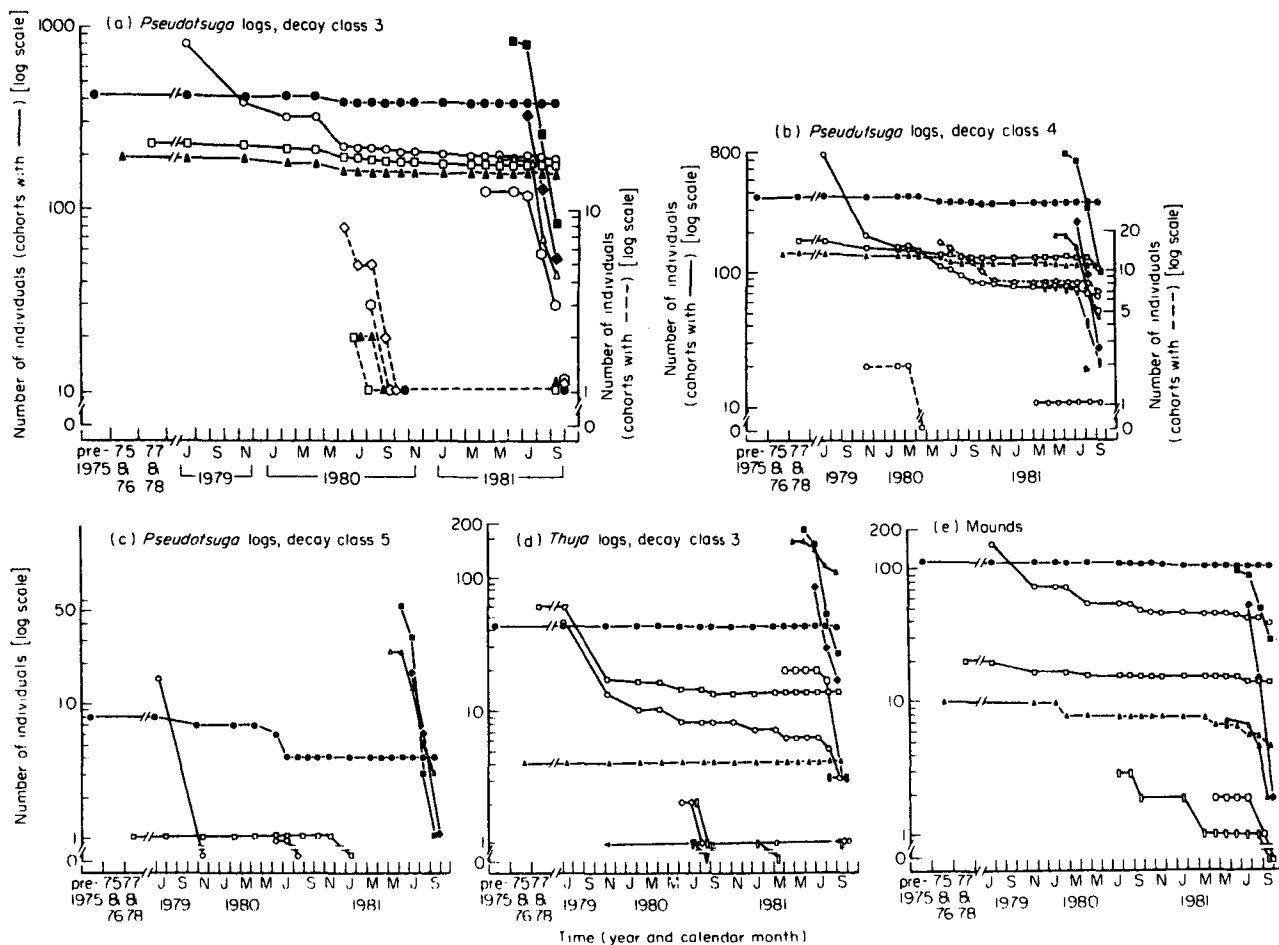
FIG. 3. Survivorship curves for cohorts of *Tsuga heterophylla* juveniles in an Oregon forest on *Pseudotsuga* logs and *Thuja* logs of various decay classes and on mounds. Right-hand scale in (a) and (b) is for cohorts plotted with hatched lines, left-hand scale for those with solid lines. Different symbols signify different cohorts.
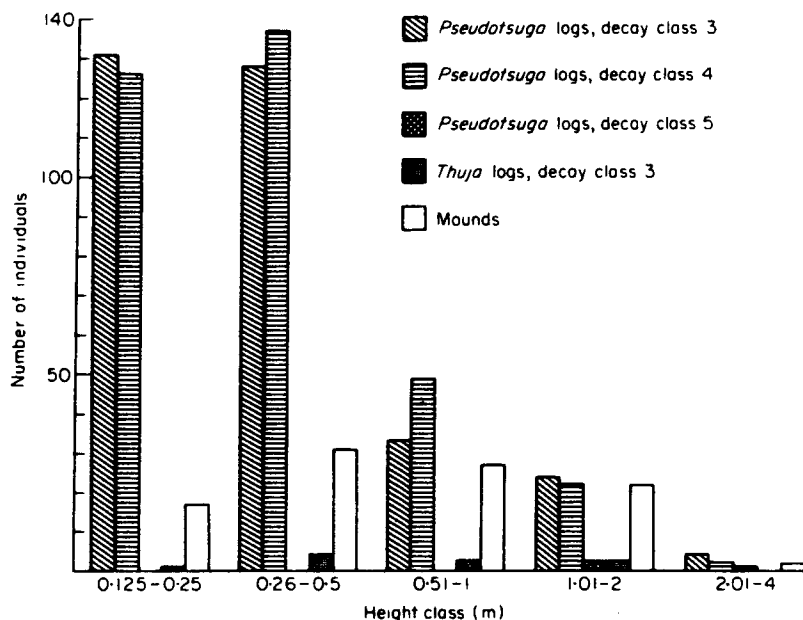
FIG. 4. Distribution by height classes of juveniles of *Tsuga heterophylla* found on five substrata in an Oregon forest in August 1980. Individuals <12·5 cm were not included in the sample.

previous 3 months. In 1981, cohorts on each substratum experienced a peak in mortality in August, except on mounds, where the death rate was highest in September.
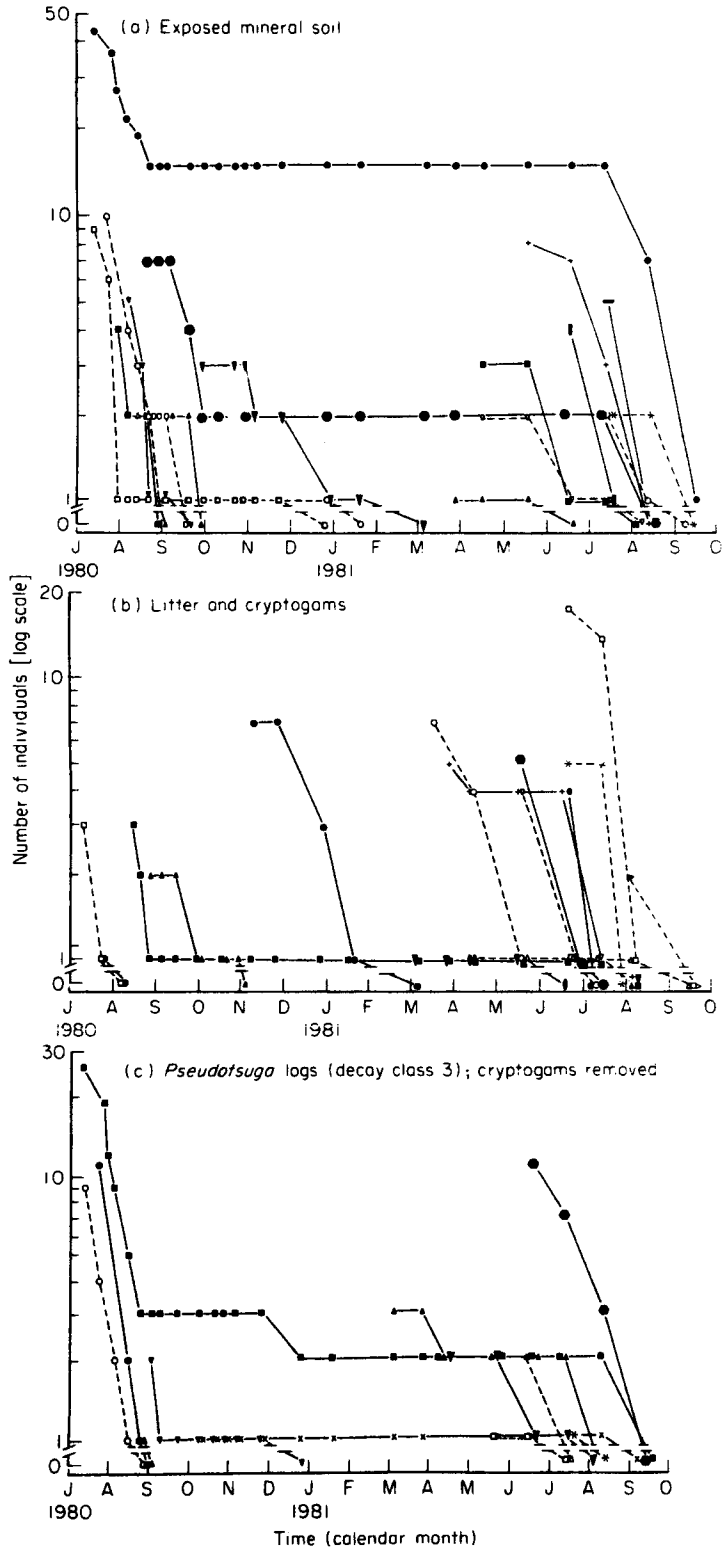
With some exceptions (e.g. pre-1975 and 1977 and 1978 cohorts on *Pseudotsuga* logs of decay class 5 (Fig. 3c), and the 1977 and 1978 cohort on *Thuja* logs (Fig. 3d), few plants of the three annual cohorts of *Tsuga*, which had emerged prior to 1979, died. The 1979 cohort of *Tsuga* juveniles on *Pseudotsuga* logs of decay class 5 was eliminated within the same year it emerged (Fig. 3c). On *Thuja* logs, the 1979 cohort decreased throughout the study (Fig. 3d). On the *Pseudotsuga* logs of decay classes 3 and 4 and on mounds. the 1979 cohorts had a low death rate by the second growing season (Figs. 3a, b).

Seedlings which emerged in 1980 or 1981 (the youngest plants included in the study) generally had the highest death rate of any category of juveniles. With very few seedlings emergent in 1980, these cohorts were greatly reduced by the end of the study regardless of substratum. Even the much larger cohorts emergent in 1981 were reduced substantially by September.

As an additional index of survival among the various substrata the height distribution was recorded in August 1980 for juvenile *Tsuga* on the twenty-six logs and five mounds (total area 441 m^2) included in the censuses. *Pseudotsuga* logs of decay classes 3 and 4 supported 86% and mounds supported 13% of those juveniles of *Tsuga* more than 12·5 cm tall (Fig. 4). Other substrata supported either few or no conifer juveniles in any height class (e.g. *Tsuga* logs of decay class 5).

Recruitment and survival of seedlings derived from sown seeds

Five weeks after seeds had been sown, emergence was observed in at least one plot for each of the nine treatments. Although 80% of the seeds from the collection germinated in laboratory trials. the highest recruitment in the field (57%) was on mineral soil. Among

(a) Exposed mineral soil

(b) Litter and cryptogams

(c) *Pseudotsuga* logs (decay class 3); cryptogams removed

Number of individuals [log scale]
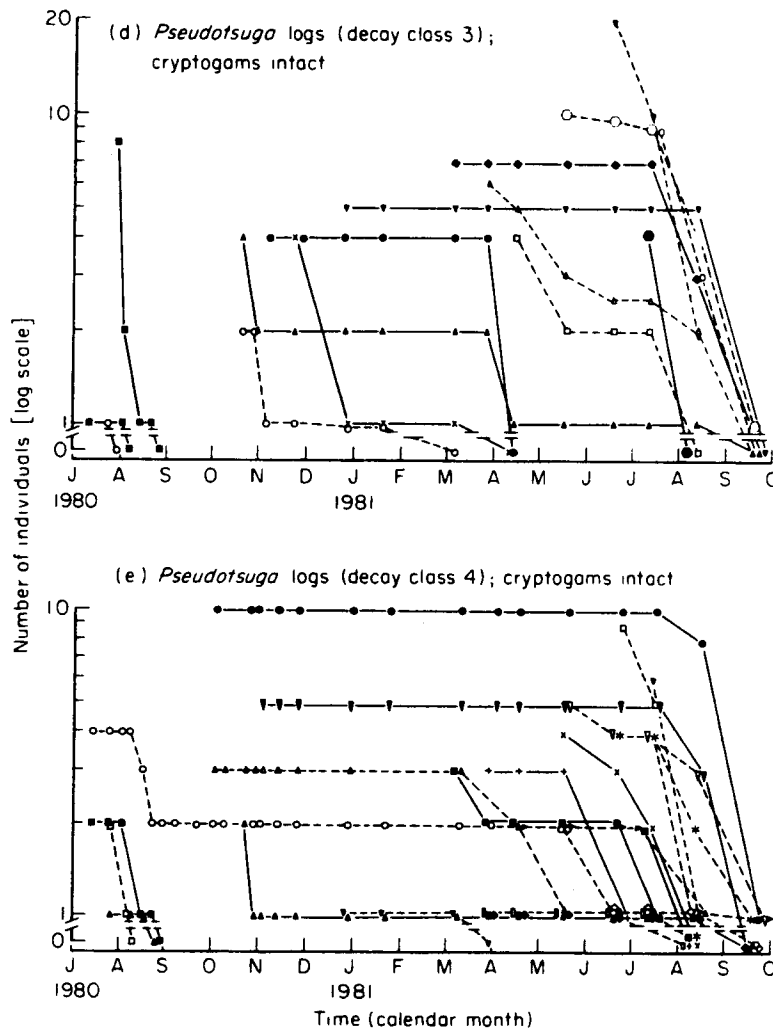
Time (calendar month)

1980   1981

Fig. 5 (a–e). Survivorship curves for seedling cohorts of *Tsuga heterophylla* emergent from sown seeds on five of the nine substrata examined in an Oregon forest. Seedlings emerging inside rodent exclosures on the substrata are shown by filled symbols and solid lines. Seedlings emerging in open plots are shown by unfilled symbols and hatched lines. Different symbols refer to different cohorts (spaced at 2-monthly intervals). Seedlings emergent from the control plots (no seed sown) established in March 1981 are designated by *.

plots not covered with a wire mesh exclosure, recruitment on *Pseudotsuga* logs of decay class 3 was higher than on other substrata, although there were no significant differences for the percentage emergence among any cohorts on these substrata. Percentage emergence on all substrata, however, was significantly higher ($P < 0.05$) when seed predation was eliminated with exclosures (Table 3).

In contrast with the results for seedling emergence, cohorts showed great variation in survival among the nine substrata (Fig. 5). Generally there was greater survival over the first 12 months after emergence among those seedlings which emerged within a cryptogam cover on logs in decay classes 3 or 4, especially those emergent in autumn (Fig. 5d, e). In

TABLE 3. Effects of substratum on emergence of seedlings of *Tsuga heterophylla* in an Oregon forest (analysed by analysis of variance), and percentage emergence of seeds inside and outside rodent exclosures on the same substrata. Symbols: N.S., no significant difference among substrata alone; *, significant difference ($P \leqslant 0.05$) between percentage emergence under exclosures versus open plots. Values not followed by the same superscript letter are significantly different ($P \leqslant 0.05$) according to 2×9 factorial analysis of variance and least significant difference tests.

	S.S.	d.f.	F
Substrata	0·041	8	1·25 N.S.
Seed predation	0·101	1	24·97*
Interaction	0·036	8	1·10 N.S.
Error	0·146	36	

	Percentage emergence	
Substratum	Open	Exclosure
Mineral soil	7·9[a]	57·13[b]
Litter, cryptogams and herbaceous plants	1·7[a]	13·3[b]
Litter and cryptogams	8·1[a]	20·0[b]
Pseudotsuga logs:		
decay class 3, cryptogams removed	3·0[a]	40·0[b]
decay class 3, with cryptogams	11·5[a]	27·3[b]
decay class 4, with cryptogams	7·8[a]	22·0[b]
decay class 5, with cryptogams	3·7[a]	24·8[b]
Thuja logs:		
decay class 3, cryptogams removed	4·9[a]	17·9[b]
decay class 3, with cryptogams	7·4[a]	24·6[b]

contrast, many seedlings emergent in litter (both with cryptogams and cryptogams plus herbaceous plants) died soon, regardless of the month of emergence (Fig. 5b). Seedlings protected from predation lingered in plots with litter (Fig. 5b). Similarly, survival on mineral soil was influenced strongly by post-emergence predation (Fig. 5a). Some cohorts in open plots as well as in exclosures displayed Deevey Type I survivorship curves, indicating that post-emergence predation was not the dominant mortality agent among cohorts (Fig. 5e). Nevertheless, cohorts within exclosures generally survived longer and had lower death rates than cohorts emerging in the same month on open plots (Fig. 5c). Cohorts emergent in June–September (both in open plots and exclosures) most often displayed an initial precipitous decline, often resulting in the termination of the cohort within 2 months (e.g. Fig. 5d).

This experiment was begun in 1980, a year in which seed production by *Tsuga* was very low. Consequently, we assume that those *Tsuga* seedlings, newly emergent in the plots, germinated from the seeds sown in June 1980. Recruitment in 1981 was from remaining viable seeds as well as the natural seed rain onto the established plots.

DISCUSSION

Demography of juvenile Tsuga heterophylla

Recruitment of many species, including conifers, is not restricted to only a few days per year but may extend over months (Harper 1977). The seasonally-changing environment results in differences in the survival of one cohort compared with survival in an overlapping cohort. For example, seedlings first detected on *Pseudotsuga* logs of decay class 4 in March 1981 all survived during the following summer while seedlings emerging on the same logs in spring and summer 1981 declined exponentially (Fig. 3b). Similar variation in survival

among cohorts was also seen among the seedlings emergent from sown seed on *Thuja* logs. Wherever data are sufficiently detailed, substantial variation has been detected in the population dynamics among cohorts emergent in the same growing season or calendar year (Baskin & Baskin 1972; Regehr & Bazzaz 1979: Mack & Pyke 1983). Emergence spread over months instead of days confers survival value to those species. particularly perennials, which do not display indeterminate growth systems (Harper & White 1974). For any mixed-age population the risk from a particular age-specific mortality agent may be ameliorated.

Juveniles of *Tsuga* do not have an equal death risk regardless of age. Cohorts less than 2 yr old in both the naturally-occurring population and the population emerging from sown seeds declined exponentially. In contrast, plants which survived the first 2 yr (pre-1979 cohorts) after germination generally experienced a low death risk for at least an additional 2 yr. Only the 1977 and 1978 cohort on *Thuja* logs (decay class 3) deviated from this pattern, as this cohort was reduced by more than 70% during summer 1979.

Elsewhere *Tsuga* also experiences generally low first-year survival. Haig, Davis & Weidman (1941) found a 61% mortality rate (based on the initial seedling cohort) between the first and second year for *Tsuga* in stands cleared of all timber, but with generally favourable sites for seedling establishment in northern Idaho. The very long census records for *Tsuga canadensis* collected by Friesner & Potzger (1944) are particularly useful in illustrating that each additional year of life imparts an increased chance of living yet another year. In that study the number of seedlings which emerged in three consecutive years on the same site were monitored twice a year from April 1932 until October 1940 (Fig. 6). Unfortunately, additional seedlings were added to each cohort during perhaps as many as six of the early censuses resulting, for example, in more individuals in the sample of a cohort in April 1933 than in the previous October. Nevertheless, in eight of fourteen 6-month periods from October 1933 onward, the period for which there are unequivocal
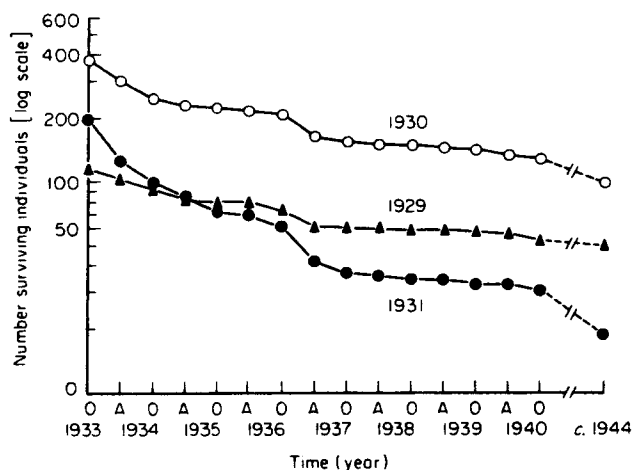

FIG. 6. Survivorship curves for cohorts of *Tsuga canadensis* which emerged in (▲), 1929: (O), 1930 and (●) 1931: as constructed from the data of Friesner & Potzger (1944). Census of some individuals began in October 1930. although survivorship may be depicted accurately only from October 1933. as unknown numbers of individuals apparently were added to the cohorts during 1931–33. O: October. A: April. See text for further explanation.

survivorship data, death rates were in the order: youngest cohort > intermediate age cohort > oldest cohort, with most deaths attributed to unseasonal drought in some summers.

A pattern of declining death rate with time for the dominant or future dominant of a site has also been observed for *Abies balsamea* in Ontario (Hett & Loucks 1976), *Acer saccharum* (Hett & Loucks 1971) in *Acer/Tilia* forest in Wisconsin, angiosperm trees in eastern United States (Good & Good 1972), and tropical forest species (Sarukhán 1978). In contrast, seral *Pinus taeda* has a constant death risk for saplings greater than 1·25 cm dbh (Christensen & Peet 1981). The demographies of too few species, however, have been examined to establish whether decreasing mortality rate always characterizes the dominants as succession advances in forests (Harper 1977).

Whilst the cause of seedling death was not specifically studied here, some field observations are pertinent. Predation is probably important because more than half of all losses were through missing (and presumably removed) plants. Yet in nearby clear-cut stands animal grazing accounted for only 11% of the 90% mortality among year-old seedlings of *Tsuga* (Gashwiler 1971). Seed predation also is extensive (Table 3), in part due to the mouse *Peromyscus maniculatus* (Wagner) which regularly forages across logs as well as in the canopy (Maser *et al.* 1981). None of the seedlings in the censuses appeared to be infected with parasitic fungi, although mycorrhizal fungi were commonly observed (Christy, Sollins & Trappe 1982). Haig (1936) also found few deaths among seedlings of *Tsuga* to be caused by fungi, although fungal infestation was the most important biotic source of mortality. Insect herbivory of seedlings is apparently minor as no seedlings appeared to have been defoliated.

For juveniles less than 5 yr old, collapse through apparent desiccation was commonly observed in summer. Such death occurred during July and August when rain often falls for only 2–3 days per month for a monthly total of less than 20 mm (J. Moreau, personal communication). Desiccation did not kill juveniles greater than 5 yr old. Gashwiler (1971) attributed more deaths to a combination of drought and heat injury than to predation among *Tsuga* seedlings in clear-cut sites near our study site. Haig (1936) drew largely similar conclusions even for seedling populations in 'full-shade' stands in the northern Rockies. Drought alone (as inferred from below average rainfall) correlated with peaks in the seedling death rate for *Tsuga canadensis* in Indiana (Friesner & Potzger 1944).

Survival in relation to the substratum mosaic

These results support the conclusion that decaying logs provide elevated 'safe sites' (*sensu* Harper, Williams & Sagar 1965) in a forest understorey where seedling establishment is otherwise thwarted by litter burial. Occurrence of juveniles in litter is sufficiently infrequent that none or very few were found in the two censuses which included non-woody substrata (an initial census in the Lookout Creek stand in July 1979 and the census in Reference Stand 7). Since survival is generally highest on logs of decay class 4 (Table 2, Fig. 4), more than simple shedding of litter is involved. No juveniles of *Tsuga* were found on any logs of decay classes 1 or 2 in this study, although Sollins (1982) reports that tree seedlings may occur on logs of decay class 2. At the one extreme, a newly fallen log (decay class 1) has maximum ability to shed litter but otherwise provides few of the features of safe sites. With decomposition to decay class 5, the log has lost features important to seedling establishment, including the ability to shed litter. Decay class 4 logs are sites for maximum establishment because these prostrate trunks are still elevated above the forest floor, thereby shedding litter, yet so decomposed that seedling lodgement is possible and nutrients in the sapwood are available to invading root systems.

As a result, the age-class distribution of juveniles at any one time (and consequently much of the likely future status of the species in the community) becomes a function of woody tissue turnover as this determines the relative area of the forest floor covered by each decay class of wood. Franklin & Hemstrom (1981) also report a correlation between the sites of highest density of coniferous seedlings and the location of logs with such intermediate stages of decay. In addition to *Tsuga*, *Picea sitchensis* and *Thuja* routinely establish on woody debris in the Pacific Northwest (Franklin & Dyrness 1973). A similar sensitivity to litter burial may also occur for *Tsuga canadensis* (Friesner & Potzger 1944), for which recruitment is largely confined to steeper slopes or level sites with sparse litter. Neither of the two decay classifications used here (Graham 1981; Sollins 1982) were designed specifically to quantify the micro-environment within which seeds and seedlings reside, yet much of the spatial variation in survival within the stand would have been undetected had the analysis been limited to simply comparing results between undifferentiated sites of woody debris and the forest floor matrix.

Frequent establishment of *Tsuga* juveniles on *Pseudotsuga* logs may illustrate one of the mechanisms by which *Tsuga*-dominated forests develop. With disturbance of a *Tsuga* habitat type, *Pseudotsuga* commonly invades and becomes a seral dominant (Franklin & Dyrness 1973). As the canopy of *Pseudotsuga* develops, light reaching the soil surface is diminished and recruitment of *Tsuga* increases (Minore 1979). As this study illustrates, *Pseudotsuga* plays an additional role in facilitating the eventual dominance of *Tsuga* through decay of *Pseudotsuga* logs. Death of any *Pseudotsuga* adult accelerates its replacement because one seed source of *Pseudotsuga* is thereby eliminated, while simultaneously an additional potential site for *Tsuga* establishment is created. Late in succession, as *Tsuga* occupies progressively more of the canopy, further increased shade restricts *Pseudotsuga* recruitment (Munger 1940). Nevertheless, the influence of the large debris accumulations from the demise of *Pseudotsuga* may influence the developing *Tsuga* community throughout its occupation of the site (Franklin & Hemstrom 1981). The last *Pseudotsuga* adult may persist for centuries while a log may decompose to decay classes 3 and 5 in less than 60 and less than 200 yr, respectively (Graham 1981). If more than 500 yr elapsed between each large-scale disturbance in these stands, the overall recruitment of *Tsuga* seedlings might be lowered as *Tsuga* logs would become the major woody debris in the understorey. However, the likelihood of no significant disturbance for more than 700 yr is probably remote (Franklin & Hemstrom 1981).

Whilst in general terms, such linkage between the turnover rate of debris and population dynamics probably exists in many terrestrial communities, the relationship is reinforced here, because large leaf litter production precludes the availability of many sites for seedling establishment. A similar negative influence of tree leaf litter on seedling emergence and subsequent survival occurs in other forests (Sydes & Grime 1981 and references therein). The example studied here may be unusual only in that different rates of seedling survival may be linked readily to a scale of specific characteristics of the community mosaic. Attention to such a scale may further substantiate Watt's (1947) view of the regeneration complex as the appropriate level to examine community change.

ACKNOWLEDGMENTS

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