

## Seed production in forests of *Chamaecyparis lawsoniana*

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In 3 years of seed collection throughout the range of *Chamaecyparis lawsoniana* (A. Murr.) Parl., 30 seed crops varied from 20 000 to 4 600 000 seeds per hectare. The overall mean was 829 000 seeds per hectare per year. Annual production per square metre of basal area (BA) varied from 600 to 185 000. Only 6 of 30 seed crops exceeded 50 000 seeds/m<sup>2</sup> BA per year but these were produced by the youngest (65 year old) and oldest (450+ year old) stands and throughout the environmental range of the species. Of other seed crops, 11 had 10 000-50 000 seeds/m<sup>2</sup> BA per year and 13 had fewer than 10 000 seeds/m<sup>2</sup> BA per year. Year-to-year variation had a local, not regional, pattern. An open-forest community produced more seed per square metre of basal area than a denser one at two mixed evergreen zone sites. Seedfall peaked from October to November, with a smaller spring peak, but some seeds fell throughout the year. Most sites differed little in the timing of peaks. Germination of trapped seed from seven sites in 1 year was 11-44% and showed no correlation with crop size. Other species in this genus produce many more seeds per hectare than *C. lawsoniana* but there is no evidence that seed production limits reproductive potential of this species. In mixed forests, *C. lawsoniana* and especially *Tsuga heterophylla* (Raf.) Sarg. were over represented in the seedfall (compared with their basal area), whereas *Pseudotsuga menziesii* (Mirb.) Franco and *Abies concolor* (Gordon and Glend.) Lindl. ex Hildebr. produced less than their share.

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Au cours de 3 années de collection de semences dans l'aire entière de répartition de *Chamaecyparis lawsoniana* (A. Murr.) Parl., 30 récoltes ont donné des rendements variant de 20 000 à 4 600 000 de semences par hectare. La moyenne d'ensemble était de 829 000 semences par hectare. La production annuelle par mètre carré de surface terrière (BA) variait de 600 à 185 000 semences. Seulement 6 des 30 récoltes dépassèrent 50 000/m<sup>2</sup> BA par an mais ces rendements furent obtenus dans les peuplements les plus jeunes (65 ans) et les plus vieux (450 + ans), dans l'aire entière de l'espèce. Parmi les autres récoltes, 11 fournirent de 10 000 à 50 000 semences/m<sup>2</sup> BA par an et 13 en fournirent moins de 10 000. On a observé des variations annuelles locales, plutôt que régionales. Une forêt ouverte a produit plus de semences par mètre carré de surface terrière qu'une forêt plus dense, à deux stations de la zone de forêt mixte coniférienne. La chute des semences atteint un maximum en octobre à novembre, avec un pic de production plus faible au printemps; mais on a observé la chute de quelques semences tout au long de l'année. Peu de différences ont été observées quant aux périodes de chute maximale. Le taux de germination des semences recueillies dans sept stations au cours d'une année était de 11-44%, sans corrélation avec l'importance de la récolte. D'autres espèces au sein de ce même genre ont produit bien plus de semences par hectare que *C. lawsoniana*, mais rien n'indique que la production de semences limite le potentiel reproductif de cette espèce. En forêts mixtes, la production de semences de *C. lawsoniana* et en particulier de *Tsuga heterophylla* (Raf.) Sarg. était très élevée (en comparaison de leur surface terrière), alors que celle de *Pseudotsuga menziesii* (Mirb.) Franco et d'*Abies concolor* (Gordon et Glend.) Lindl. ex Hildebr. était médiocre.

[Traduit par le journal]

### Introduction

*Chamaecyparis lawsoniana* (A. Murr.) Parl., Port Orford cedar, is a valuable forest tree within its small geographic range in southwestern Oregon and northwestern California. It is ecologically versatile, occupying a variety of communities and environments (Whittaker 1960; Hawk 1977). It is a pioneer in

most habitats but also continues to reproduce in old-growth forests, being tolerant to both shade and fire (Hawk 1977).

A knowledge of seed production by conifers is important for practical reasons as well as for understanding their ecology. For example, lack of seed production by old *Chamaecyparis* trees in Taiwan has been suggested as a cause of poor regeneration of old-growth forests (Lee 1962). The one study of seed

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production of *C. lawsoniana* (Hayes 1958) was limited to a small area, in stands of undefined nature, and the collection times were several months apart. More information about seedfall is necessary to assess its importance in controlling the ecological behavior and the regeneration after clearcutting of *C. lawsoniana*. Considering the wide range of environments where the species grows (Zobel and Hawk 1979), seed-crop size and timing of seedfall might be expected to vary greatly among habitats.

This paper reports the total seedfall, seedfall per unit basal area, timing of seed release, and germination percentage of the seed captured, for 12 sites selected to represent the range of habitats of *C. lawsoniana*. This is part of a study of the ecology of *Chamaecyparis* in cooperation with the Taiwan Forestry Research Institute.

### Methods

Seeds were collected periodically between September 1974 and September 1976 from 11 sites (Fig. 1, Table 1). At the 12th site, in Brewer Spruce Research Natural Area (Franklin *et al.* 1972), seeds were collected only once each year. In

1976–1977 the total seed crop at the six northern sites had accumulated before collection.

Seed traps used (Herman 1963) measured  $0.305 \times 0.610$  m ( $1 \times 2$  ft). Nine to 21 traps were placed in each stand on a  $10 \times 10$  m grid, with the trap surface horizontal. One collected seed was the equivalent of 2562 (with 21 traps) to 5980 seeds (with 9 traps) per hectare. At Agness Pass and Pine Point, two communities were sampled (Table 1). Thermographs were located within the seed-trap array except in the Brewer Spruce and younger Grayback stands.

Seeds were collected approximately once a month except in the summer of 1975 and at sites where snow covered the traps. The monthly samples from a site were usually combined and counted. However, the April 1976 collection at Coos County Forest and the entire 1976–1977 catch at the six northern sites were counted by individual trap. The monthly seed catch from sites with enough seeds to test in 1975–1976 was germinated on filter paper in petri plates in the laboratory at  $20^\circ\text{C}$  (range  $16$ – $22^\circ\text{C}$ ), with room light 9 h a day. Tests ran 3–5 weeks and ended after a week with no germination.

Basal area of each tree species (over 15 cm diameter at breast height (dbh)) in each stand was measured using a wedge prism, with each trap as a sample point. The effectiveness of trees on a site in producing seeds was expressed as the annual seedfall per square metre of basal area of each species.

Linear regression and correlation were used to relate seed-crop size to stand and habitat characteristics, and to relate seeds per trap to surrounding basal area. Least significant difference and *t*-tests were used to determine significance of differences among years and species at the same site, and among vegetation zones and types of parent material. Significance was judged at the  $p = 0.05$  level.

### Results

#### *Chamaecyparis lawsoniana* Seed Production

Annual seed production varied greatly from site to site and year to year (Table 2), from 20 000 to 4 600 000 seeds per hectare and from 600 to 185 000 seeds per square metre of basal area. High annual seed production occurred at sites representing the range of environments occupied by *Chamaecyparis lawsoniana* (Tables 1 and 2) in coastal and inland sites, high and low elevations, old and young stands, and open and dense forests, and on all major geologic substrates. Neither the averages of seedfall per hectare nor those of seedfall per square metre of basal area were significantly related to stand age, elevation, latitude, vegetation zone, type of parent material, mean annual air temperature, or average maximum air temperature in July. Mean seedfall per hectare was not significantly related to basal area in the stand.

Of the 30 seed crops collected, 6 were moderate to heavy, 11 were light, and 13 were very light (Fig. 2). Six sites lacked moderate or heavy seed crops and no site had more than one moderate or better crop. There was little correspondence between geography and year-to-year change in seed-crop size (Figs. 1 and 2). The similar Grayback stands (Fig. 2) are less than 1 km apart. However, from 1974–1975 to 1975–1976,

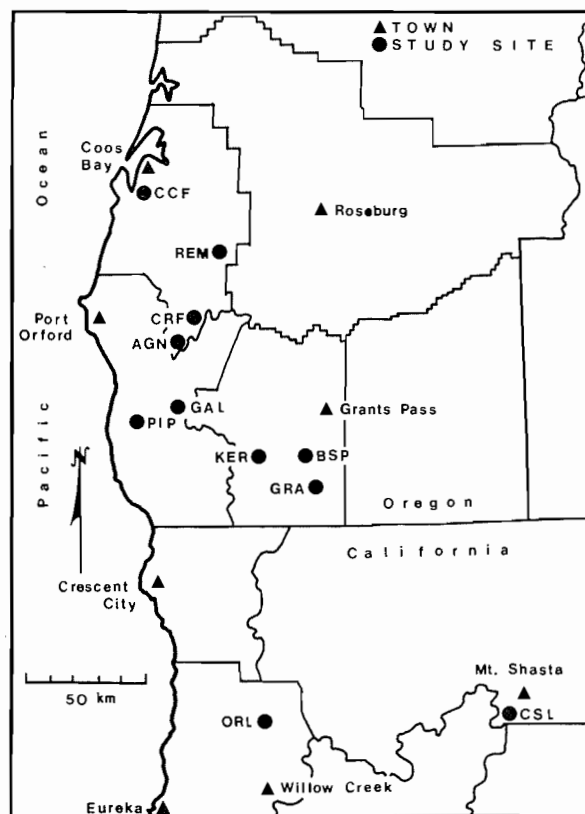


FIG. 1. Location of study sites. See Table 1 for site names and characteristics.

TABLE 1. Characteristics of stands sampled. Zones are named according to Franklin and Dymess (1973); Communities are described by Hawk (1977). Species abbreviations: Chla, *Chamaecyparis lawsoniana*; Tshe, *Tsuga heterophylla*; Psme, *Pseudotsuga menziesii*; Abco, *Abies concolor*; Pije, *Pinus jeffreyi*; Pila, *P. lambertiana*; Pimo, *P. monticola*; Pisi, *Picea sitchensis*; Abma, *A. magnifica* var. *shastensis*; Cade, *Calocedrus decurrens*; geologic types: SED, sedimentary; UM, ultramafic; Zone: ME, mixed evergreen

Site name	Site abbrev.	Elev. (m)	Dominant tree age (years)	Basal area (m <sup>2</sup> /ha)							Geologic type	Veg. zone	Plant community	No. of traps
				Chla	Tshe	Psme	Abco	Pije	Pila	Others				
Coos Co. Forest	CCF	70	65	25.3	5.2	12.6				Pisi 16.3	SED	Pisi	Sandstone	16
Remote	REM	500	100	14.4	6.9	23.6					SED	Tshe	Swordfern	16
Coquille River Falls	CRF	520	450+	44.5	6.9	17.2					SED	Tshe	Swordfern	16
Agness Pass	AGN	870	110-180	8.5		7.9		4.6	8.3		UM	ME	Tanoak and mixed pine	20 (18)*
Pine Point	PIP	600	60-230	10.6		3.1		4.9	0.5		UM	ME	Tanoak and mixed pine	21 (18)*
Orleans	ORL	830	370	36.7		27.0					Other	ME	Tanoak	16
Kerby	KER	360	300	6.7		1.7		0.9	0.6	Cade 2.2	UM	ME	Mixed pine	16 (11)*
Game Lake	GAL	1280	170	30.9		47.4					UM + other	Abco	White fir	17
Castle Lake	CSL	1520	300+	62.3			9.7			Pimo 12.9	Other	Abco	White fir	16
Grayback														
Upper	GRA(U)	1420	450+	31.3		24.1	13.5			Abma 2.3	Other	Abco	Mixed fir	16
Lower	GRA(L)	1280	250 (80)†	14.7		30.8	5.5			Pimo 2.8	Other	Abco	Mixed fir	10
Brewer Spruce RNA	BSP	1340	390	39.8		33.2	0.5				Other	Abco	Mixed fir	9

\*Some traps stolen during study.

†Older Chla over young trees of other species.

TABLE 2. *Chamaecyparis* seed production characteristics of the 12 sites. BA, basal area

Site	Annual seedfall ( $\times 10^3$ )						Mean of seeds/year ( $\times 10^3$ )	
	1974-1975		1975-1976		1976-1977		per hectare	per square metre BA
	Seeds/ha	Seeds/m <sup>2</sup> BA	Seeds/ha	Seeds/m <sup>2</sup> BA	Seeds/ha	Seeds/m <sup>2</sup> BA		
CCF	215	8.5	4622	182.7	138	5.5	1658	65.5
REM	78	5.4	78	5.4	72	5.0	76	5.3
CRF	2409	54.1	718	16.1	350	7.9	1159	26.0
AGN	171	20.2	107	12.6	93	10.9	124	14.5
PIP	111	10.5	82	7.7	1594	150.4	596	56.2
ORL	374	10.2	20	0.6			197	5.4
KER	1239	184.9	332	49.5			786	117.3
GAL	89	2.9	655	21.1	41	1.3	262	8.5
CSL	1990	31.9	272	3.5			1131	18.2
GRA(U)	321	10.3	4511	144.1			2216	70.8
GRA(L)	78	5.3	2277	154.9			1178	80.1
BSP	114	2.9	1017	25.6			566	14.2
Means of Vegetation Zones								
Pisi + Tshe	901	22.7	1810	68.2	187	6.1	965	32.3
ME	474	32.0	135	17.6	844	80.7	426	48.4
Abco	518	10.7	1746	69.8			1071	38.4
Overall mean							829	40.2

seed crops increased at sites with the coolest summers and decreased most at the warmest site; change in seed-crop size at a site was significantly related to its average maximum temperature for July ( $r = -0.76$ ,  $n = 11$ ).

At Pine Point and Agness Pass two plant com-

munities were sampled (Table 1) but data were combined in Table 2. In all cases seed production per unit basal area was greater in the more open stands at these two sites (Table 3); the 1976-1977 production in the Pine Point Mixed Pine stand was higher than any in Table 2. Wind-blown seed from the nearby Tanoak community probably inflated this value. At Agness Pass the Mixed Pine stand had its highest production when the adjacent Tanoak community had its lowest.

In closed forests, five of seven seed crops counted by trap showed no correlation between seed catch per trap and basal area of *Chamaecyparis* around the trap. However, both the April 1976 and the total 1976-1977 collection at Coos County Forest showed a significant positive correlation ( $n = 16$ ,  $r = 0.72$  and  $0.56$ ). Open stands at Agness Pass and Pine Point with single trees or clumps acting as point sources of seed also showed a significant relationship between seed catch and basal area near the trap ( $n = 10$  and  $11$ ;  $r = 0.61$  and  $0.70$ ).

Maximum rates of seedfall (number of seeds per hectare per day) during a single collection period were below 10 000 except in 1974-1975 at Coquille River Falls (29 300) and in 1975-1976 at Coos County Forest (85 800) and the two Grayback sites (30 000 and 13 100).

#### Timing of *Chamaecyparis* Seedfall

Timing of seedfall differed considerably in 1974-1975 and 1975-1976 (Fig. 3). At all seven sites where

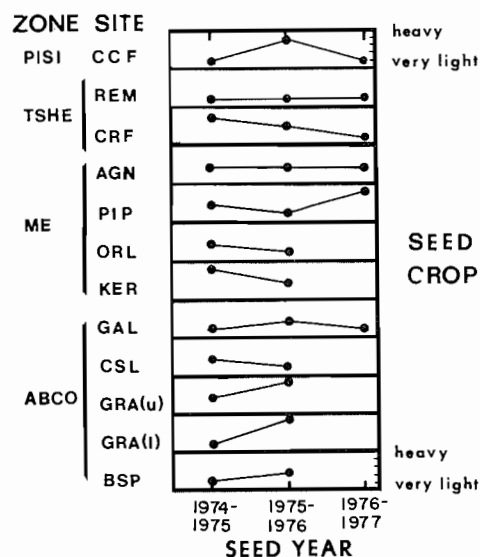


FIG. 2. Pattern of occurrence of *Chamaecyparis* seed crop size for the 30 seed crops. Seed crop size is defined by the number of seeds produced annually per square metre of tree basal area:  $> 100\,000$  = heavy;  $50\,000$  to  $100\,000$  = moderate;  $10\,000$  to  $50\,000$  = light; and  $< 10\,000$  = very light.

TABLE 3. A comparison of seed production per square metre of basal area in the open Mixed Pine and more dense Tanoak communities at Pine Point and Agness Pass

Site	Community	<i>Chamaecyparis</i> basal area, m <sup>2</sup> /ha	No. of traps	Annual seed production (no. of seeds $\times 10^3$ )		
				1974-1975	1975-1976	1976-1977
PIP	Tanoak	29.1	6	7.4	4.0	57.7
	Mixed pine	2.7	11-15	31.4	14.4	572.2
AGN	Tanoak	14.7	8-10	16.5	10.4	0.9
	Mixed pine	2.3	10	43.7	25.0	74.9

winter collection was fairly consistent, seeds were more concentrated in peaks in 1975-1976. Peaks were earlier in 1975-1976 at five of these seven sites. By mid-January 54% of the total seed had fallen in 1974-1975 compared with 62% in 1975-1976;

figures for late April were 83 and 89%, respectively.

Overall seedfall had two peaks, the later one being the smaller (Fig. 3). Only Kerby had a pattern distinctly contrary to Fig. 3; it had three peaks in 1974-1975 and the later peak was the largest in both years. Some seed fell during the summer at most sites. The new seed crop started to fall in September. In general, timing of seedfall was more similar among sites than might be expected given their very different environments.

Comparison of periodic seedfall with temperature at the sites (measured in the understory) or with percentage of days with rainfall recorded at the nearest weather station during the collection period showed no discernible relationship.

#### Germination of *Chamaecyparis* Seeds

Average germination in the laboratory was highest for seeds from the *Abies* zone and lowest for Kerby and Coos County Forest (Table 4). When only germinable seed is considered, the Grayback sites were the most productive. Seeds collected early and late germinated less than those which fell during and between the two peaks of seedfall. Germination percentage was not significantly correlated with seed-crop size, in contrast to that of *C. thyoides* (Little 1950).

TABLE 4. Mean germination and calculated germinable seed crop for seed collected in 1975-1976

Site	Mean germination, %	Germinable seed crop, seeds per year ( $\times 10^3$ )	
		per hectare	per square metre BA
CCF	13.8	638	25.2
CRF	19.8	142	3.2
KER	11.0	36	5.5
GAL	25.6	168	5.4
CSL	24.5	67	1.1
GRA(U)	34.2	1543	49.3
GRA(L)	44.2	1006	68.5

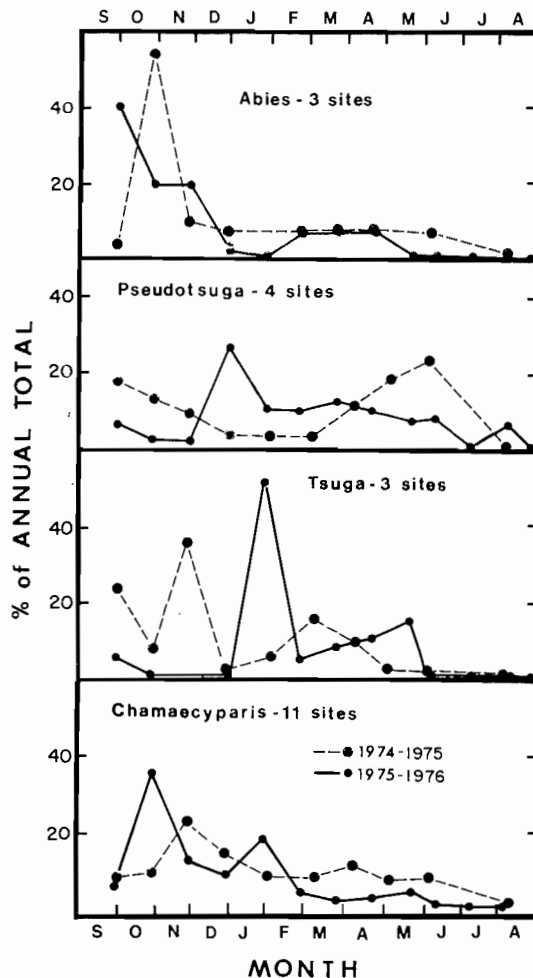


FIG. 3. Average percentage of total annual seedfall at all sites which fell during each collection period, plotted at the middate of the period.

TABLE 5. Seed production of *Tsuga heterophylla*, *Pseudotsuga menziesii*, and *Abies concolor* at different sites. Only sites with considerable seedfall in at least 1 year are shown

Species and site	Annual seedfall (no. of seeds $\times 10^3$ )						Mean annual seedfall (no. of seeds $\times 10^3$ )	
	1974-1975		1975-1976		1976-1977			
	per hectare	per square metre BA	per hectare	per square metre BA	per hectare	per square metre BA	per hectare	per square metre BA
<i>Tsuga heterophylla</i>								
CCF	1415	272.1	609	117.1	50	9.6	691	132.9
REM	205	29.8	62	9.0	0	0	89	12.9
CRF	323	46.8	248	35.9	44	6.4	205	29.7
Mean							328	54.2
<i>Pseudotsuga menziesii</i>								
CCF	31	2.5	0	0	24	1.9	18	1.5
REM	75	3.2	7	0.3	126	5.3	69	2.9
CRF	17	1.0	7	0.5	299	17.4	108	6.3
PIP	3	1.0	3	1.0	70	22.6	25	8.2
AGN	3	0.4	0	0	62	7.8	22	2.7
GAL	6	0.1	0	0	317	6.7	108	2.3
GRA(U)	17	0.7	127	5.3			72	3.0
BSP	11	0.3	96	2.9			54	1.6
Mean							59	3.7
<i>Abies concolor</i>								
GAL	19	*	0	*	6	*	8	*
GRA(U)	679	50.3	357	26.4			518	38.4
GRA(L)	43	7.8	65	11.8			54	9.8
Mean (GRA)							286	24.1

\*No basal area recorded from the trap array. Trees are on nearby slope.

Seeds collected directly from trees near the sites in September 1975 had better germination at Grayback (52%) and Coos County Forest (37%) than those from the traps, but the percentage was about the same as for trapped seeds at Coquille River Falls and Game Lake. At the open Agness Pass site, 55% of seeds collected directly from the trees germinated. *Chamaecyparis lawsoniana* is reported (United States Department of Agriculture 1974) to have germinability of 48-52%, similar to our better laboratory results.

#### Seed Production of Other Species

Sufficient seeds of three other conifers were collected (Table 5) to permit comparison with seedfall of *Chamaecyparis*. Annual seedfall of *Tsuga heterophylla* (Raf.) Sarg., western hemlock, differed from *Chamaecyparis* in timing (Fig. 3) and amount (Tables 2 and 5), although average seedfall at the three sites was not significantly different for the two species. Seeds were significantly more concentrated in the two peaks than for *Chamaecyparis* at the same sites. *Tsuga* produced two heavy seed crops in a row at Coos County Forest.

Seedfall of *Pseudotsuga menziesii* (Mirb.) Franco,

Douglas-fir, was nil to low at most sites in the first 2 years, but was considerable at five sites in 1976-1977. All five montane sites sampled for 3 years had maximum seedfall in that year (Table 5). Differences between years in periodicity of seedfall (Fig. 3) may be due to most seed being from low elevations in the 1st year and high elevations in the 2nd.

Seed fall of *Abies concolor* (Gordon and Glend.) Lindl. ex Hildebr., white fir, was very concentrated in one early season peak (Fig. 3). Most would be buried under the snowpack. *Abies* seed production per unit basal area was relatively high both years at the older Grayback stand. It was four times that at the younger stand, in contrast to the similarity shown for *Chamaecyparis* (Tables 2 and 5). This difference may be due to the fact that *Abies* at the younger stand are all less than 60 years old, whereas those at the older stand are more than 100 years old.

#### Discussion

##### Seed Crop Size

Seed production by *Chamaecyparis lawsoniana* was quite variable. However, this variability was not clearly related to the stand or site factors assessed,

TABLE 6. Seed production and germination reported for *Chamaecyparis* spp. and some conifers associated with *C. lawsoniana*. A further reference for several species is U.S. Department of Agriculture (1974)

Species	Location	Seed crops reported, million/ha		Interval between good crops, years	Germination, %	Reference
		Maximum	Other			
<i>Calocedrus decurrens</i>	California	1.0		3-6	14-65 (98)	Fowells 1965
<i>Chamaecyparis lawsoniana</i>	Oregon	3.1	1.5	3-5	48-52	Hayes 1958
<i>C. nootkatensis</i>	Alaska, Canada			≥4	0-29	Owens and Molder 1975
<i>C. obtusa</i>	Japan	98	6.5		87-91	Sato 1974
<i>C. thyoides</i>	New Jersey	22	1.2-1.9, 20	2-3	8-40	Little 1950
<i>Sequoia sempervirens</i>	California	107	27-80	Often 0	3-13	Boe 1961, 1968
<i>Thuja plicata</i>	Oregon	1.6*	Mean of 0.44	3-4	34-90	Gashwiler 1969

\*Comprises 10% of stand.

and heavy seed crops occurred over the ranges of age, geography, and habitat sampled. There was no evidence that the spread or maintenance of the species could be limited by inadequate seed production within the sampling area.

In many studies of conifer seed production, description of the stand sampled is almost ignored (e.g., 'a mature stand'). This prevents easy comparison of seedfall with results from other studies or other sites. However, to understand the ecological influence and the control of seed production, one needs to compare seedfall among stands of various ages, densities, and compositions. It is reasonable to expect long-term mean seed production to reflect the absolute importance of a species on a site to some degree; thus, data need to be expressed so that the variable capacity for seed production of different populations is taken into account. Reporting only seedfall per hectare greatly limits interpretations one can draw from the data. Basal area, used as the unit of tree importance in this study, is easily measured. For a shade-tolerant tree in stands of mixed age, as studied here, it should reflect characteristics more obviously related to capacity for seed production, such as mass or surface of the crown, which would be very difficult to measure. A quantitative description of the stand, with expression of seedfall per unit of tree importance, would be a worthwhile addition to future studies of seed production.

In a study as short as this one, in which many sites apparently produced well below their potential in all years, it is no surprise that seed production per hectare was not correlated with basal area per hectare for the entire study. Even so, use of seedfall per square metre of basal area is important in interpreting some of the results for areas which had a year of high seed production. Kerby, a hot, marginal site for *Chamaecyparis* on serpentine, had only 35% of mean seed production per hectare at the older

Grayback stand (31 km away at high elevations on good soil). Yet production per square metre of basal area at Kerby exceeds that at Grayback (Table 2), indicating that the capacity of the individuals for seed production did not decline in the marginal habitat. As another example, the older Grayback stand had 213% of the basal area (Table 1) and 188% of the seedfall per hectare of the younger stand but mean seed production per square metre of basal area for the two areas differed by only 12% (Table 2). Although the seed-production capacity of the older stand is greater, the capacity per unit of tree importance is quite similar.

Of 30 *Chamaecyparis* seed crops sampled, seed production (number of seeds per square metre of basal area) in 6 crops was over 50 000, in 11 crops was from 10 000 to 50 000, and in 13 crops was less than 10 000 (Fig. 2). No complete crop failures were observed. Assuming the study provided a representative sample of sites and years, about one seed crop in five can be expected to be moderate to heavy. This conclusion concurs with the previous statement that, although some seeds fall each year, good crops occur only once every 4-5 years (Hayes 1958).

The year-to-year pattern of seed-crop size of *C. lawsoniana* may be similar within types of habitat rather than resulting in heavy seed years simultaneously over a large geographic area. Change in seedfall from 1974-1975 to 1975-1976 at a given site was correlated with summer temperature but not geographic location. In contrast, at all five montane stands sampled for 3 years, *Pseudotsuga* produced its maximum crop the 3rd year; *Chamaecyparis* seedfall peaked at least at one of these sites in each of the 3 years (Tables 2 and 5).

Maximum seed production of some related and associated species with similar cone morphology is much higher than for *C. lawsoniana* (Table 6). This apparently low seed production of our species,

relative to similar species elsewhere, may partially reflect the purity of the stands. *Chamaecyparis lawsoniana* shared the dominance at our sites (Table 1) whereas *Sequoia*, *C. obtusa*, and *C. thyoides* were probably the only major canopy trees in these other studies.

#### Timing of Seedfall

Timing of seedfall within each season varied little among sites compared with variation in their environments (Zobel and Hawk 1979) and the phenology of primary growth (D. B. Zobel and G. M. Hawk, unpublished data), yet timing varied considerably between years (Fig. 3). Some regional phenomenon which is similar at all elevations may synchronize seed release. Passage of strong storm winds is a possibility (cf. Little 1950).

Failure to find correlation between seedfall and ambient temperature or rainfall reflects the poor relationship between patterns of humidity, temperature, and seedfall of *C. thyoides* (Little 1950) and *Thuja plicata* (Hetherington 1965). In contrast, *Tsuga heterophylla* definitely responds to humidity (Ruth and Berntsen 1955; Hetherington 1965).

Earlier studies of *Chamaecyparis lawsoniana* (Hayes 1958) and of congeneric species (Little 1950; Sato 1974) show a generally similar seasonal pattern of seed release, with a fall-to-winter peak but with some dispersal in all months. There appear to be more seeds shed after the peak for *C. lawsoniana* than for *C. thyoides* or *C. obtusa*.

#### Relationships with Associated Species

The representation of different species in the seed rain varied in this study. *Tsuga*, a heavy seeder in other areas (Gashwiler 1969), acted similarly here, averaging 27% of the seeds per crop but providing only 12% of the basal area. *Chamaecyparis* was also over represented (means of 80% seeds, 56% basal area) except at Remote, where percentage seedfall and basal area were equal. In contrast, *Abies concolor* (6% seeds, 11% basal area) and especially *Pseudotsuga* (11% seeds, 40% basal area) were under represented.

Seeds of *Tsuga* are 0.8 times as heavy as those of *C. lawsoniana*; seeds of *Pseudotsuga* are 5.4 times heavier and those of *Abies concolor* are 19 times heavier (United States Department of Agriculture 1974). Recalculating the species' representation in the average seedfall in terms of the estimated weight of seeds produced removed much of the variation. Seed weight per percentage basal area of *Pseudotsuga* was similar to *Chamaecyparis* and *Tsuga* was slightly higher. However, *Abies* was greatly over represented

when seedfall was expressed in terms of weight, in contrast to the situation with seed numbers.

Seedfall of *Tsuga* at these sites (where it was only a minor part of the stand) did not approach that reported for other areas (Godman 1953; Ruth and Berntsen 1955; Gashwiler 1969). In the southern Oregon Cascades, seedfall of *Abies concolor* at the edges of a mixed fir stand was at or above our maximum value (50 000 seeds per square metre of basal area) in two 'very heavy' seed years (calculated from data of Franklin and Smith 1974). Our data for *Pseudotsuga* include no really good years, compared with Gashwiler's (1969) data for the Oregon Cascades. His 12 year mean of 542 000 seeds/ha was well above our maximum. However, much of the difference is probably due to the greater relative importance of *Pseudotsuga* in the Cascades stand (80%) than in ours.

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- BOE, K. N. 1961. Redwood seed dispersion in old-growth cut-overs. U.S. Dep. Agric. For. Serv. Res. Note 177.
- . 1968. Cone production, seed dispersal, germination in old-growth redwood, cut and uncut stands. U.S. Dep. Agric. For. Serv. Res. Note PSW-184.
- FOWELLS, H. A. 1965. Silvics of forest trees of the United States. U.S. Dep. Agric. Handb. 271.
- FRANKLIN, J. F., and C. T. DYRNESS. 1973. Natural vegetation of Oregon and Washington. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. PNW-8.
- FRANKLIN, J. F., F. C. HALL, C. T. DYRNESS, and C. MASER. 1972. Federal research natural areas in Oregon and Washington: a guidebook for scientists and educators. U.S. Dep. Agric. For. Serv., Pac. Northwest For. Range Exp. Stn.
- FRANKLIN, J. F., and C. E. SMITH. 1974. Seeding habits of upper-slope tree species. III. Dispersal of white and Shasta red fir seed on a clearcut. U.S. Dep. Agric. For. Serv. Res. Note PNW-215.
- GASHWILER, J. S. 1969. Seed fall of three conifers in west-central Oregon. For. Sci. 15: 290-295.
- GODMAN, R. M. 1953. Seed dispersal in southeast Alaska. Alaska For. Res. Cent. Tech. Note 16.
- HAWK, G. M. 1977. Comparative study of temperate *Chamaecyparis* forests. Ph.D. thesis, Oregon State University, Corvallis, OR.



- HAYES, G. L. 1958. Silvical characteristics of Port-Orford-cedar. U.S. Dep. Agric., For. Serv. Pacific Northwest For. Range Exp. Stn. Silvical Ser. 7.
- HERMAN, F. R. 1963. Seed-trap liners of nylon tent screening. J. For. 61: 531.
- HETHERINGTON, J. C. 1965. The dissemination, germination and survival of seed on the west coast of Vancouver Island from western hemlock and associated species. B.C. For. Serv. Res. Note 39.
- LEE, S. E. 1962. Taiwan red- and yellow-cypresses and their conservation. Taiwania, 8: 1-13.
- LITTLE, S. 1950. Ecology and silviculture of whitecedar and associated hardwoods in southern New Jersey. Yale Univ. Sch. For. Bull. 56.
- OWENS, J. N., and M. MOLDER. 1975. Pollination, female gametophyte, and embryo and seed development in yellow cedar (*Chamaecyparis nootkatensis*). Can. J. Bot. 53: 186-199.
- RUTH, R. H., and C. M. BERNTSEN. 1955. A 4-year record of Sitka spruce and western hemlock seed fall on the Cascade Head Experimental Forest. U.S. Dep. Agric. For. Serv., Pacific Northwest For. Range Exp. Stn. Res. Pap. 12.
- SATO, K. 1974. *Chamaecyparis obtusa* in Japan. A partial translation by M. E. Hale. Manuscript, Oregon State University, Dep. Bot. Plant Pathol., Corvallis.
- UNITED STATES DEPARTMENT OF AGRICULTURE, Forest Service. 1974. Seeds of woody plants in the United States. U.S. Dep. Agric. Handb. 450.
- WHITTAKER, R. H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecol. Monogr. 30: 279-338.
- ZOBEL, D. B., and G. M. HAWK. 1979. The environment of *Chamaecyparis lawsoniana*. Am. Midl. Nat. In press.