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D. L. REUKEMA

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Seedfall in a young-growth Douglas-fir stand: 1950-1978

DONALD L. REUKEMA

Pacific Northwest Forest and Range Experiment Station, Forestry Sciences Laboratory, Olympia, WA, U.S.A. 98502

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A 29-year record of seedfall in thinned and unthinned portions of a Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stand, spanning ages 39 through 68, reveals annual seed production from no seeds to about 3 million per hectare. For the nine largest crops, annual seedfall in the best seed-producing thinning treatment included at least 100 000 filled seed per hectare. The first of these nine crops was in 1950; the other eight occurred at 1- to 4-year intervals beginning with 1959. For the nine largest crops, the proportion of seeds filled averaged 45%o and ranged from 30 to 54%. Typically, about two-thirds of the seed fell by mid-December; but for two of the three largest crops. time of seed shedding was greatly delayed. Thinning substantially increased the number of seeds produced in some years following thinning but the effect was not lasting. There was little or no effect of thinning on the proportion of seed filled or timing of seed dissemination.

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L'analyse de données receuillies durant une période de 29 ans sur la production de semences de Douglas, dans des portions éclaircies et non traitées d'un peuplement (dont I'âge est passé de 39 à 68 ans), révèle une production annuelle allant de 0 à 3 millions de semences à I'hectare. Pour les neuf meilleures récoltes la production annuelle dans la meilleure eclaircie d'ensemencement était d'au moins 100 000 semences pleines à I'hectare. La première des neuf récoltes eut lieu en 1950; les huit récoltes subséquentes eurent lieu à intervalles de l à 4 ans, à compter de 1959. Pour les neuf meillcures récoltes, la proportion de semences pleines s'élevait à 45% en moyenne (30 à 54%). Phénomène normal, environ les deux tiers des semences tombèrent vers la mi-décembre; mais pour deux des trois meilleures récoltes, la période de chute fut retardée. Certaines années suivant le traitement, 1'éclaircie a augmenté appreciablement la production de semences, mais 1'effet était de courte durée. L'éclaircie a eu peu ou pas d'effet sur la proportion de semences pleines on sur la période de dissémination.

[Traduit par le journal]

Introduction

The need for knowledge on the seed-production capabilities of young stands is becoming increasingly important with the current trend toward shorter rotations. These young stands must produce the seed needed for regeneration. One of the earliest studies of seedfall in young Douglas-fir stands was started in 1950 on Voight Creek Experiment Forest- in western Washington. The study was superimposed on a test of the effects of different thinning regimes on growth and yield. Four objectives of the study were (1) to determine the capacity of young Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stands to produce seed and the periodicity of their seed crops, (2) to estimate the proportion of seed filled, (3) to determine the timing of seed dissemination over the season, and (4) to assess the effects of thinning on seed production. Preliminary findings were reported by Shaw (1954) and Reukema (1961).

This paper updates findings from that study, which was terminated in 1972 after providing a 22-year record of seedfall. It supplements them with 7-year data from another study, begun in 1972, to extend information on size and periodicity of seed crops.

Study area

The experimental forest is situated in the foothills of the Cascade Range, near Mt. Rainier. Annual precipitation averages about 1270 mm, of which one-third falls during April through September. The average annual temperature is about 10°C; the April through September average is 14°C. The experimental area lies at an elevation of about 300 m. The land slopes generally to the north and west, but the gentle topography is quite variable. Soils are derived from glacial out-wash deposits and range from gravelly sand to sandy clay loam. Average site index is about 44 m.[3]

The present forest stand became established about 1912, following cutting of virgin timber and repeated burns. Althouth quite uniform, the stand exhibits typical variation in degree of stocking, stand density, and species composition. Douglas-fir accounts for more than 90% of the cubic volume. There is a scattering of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), western red cedar (*Thuja plicata* Donn ex D. Don), and

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[2] Maintained by the Pacific Northwest Forest and Range Experiment Station in cooperation with St. Regis Paper Company.

[3] Site index is the average height of dominant and co-dominant trees at age 100.

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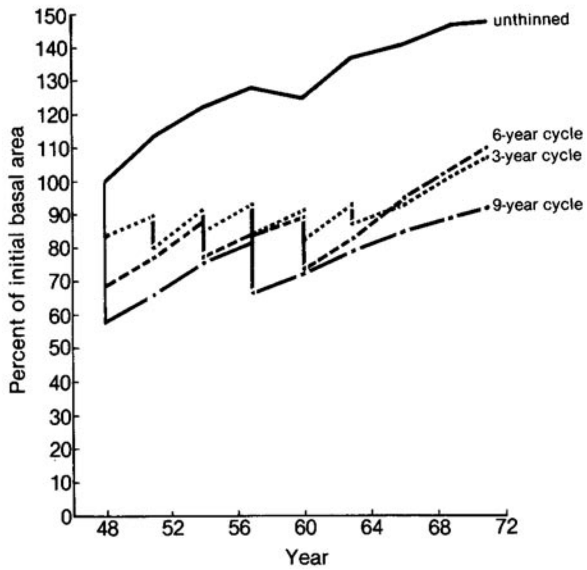

FIG. 1. Relative levels of growing stock, by thinning cycle. Percent of 1948 basal area before thinning.

bitter cherry (*Prunus emarginata* Dougl. ex Eaton) throughout the stand and red alder (Alnus rubra Bong.), bigleaf maple (*Acer macrophyllum* Pursh), and black cottonwood (*Populus trichocarpa* Torr. & Gray) occur in moist areas.

Thinnings were begun in the fall of 1948, when the stand was 37 years old. Four regimes were applied to contiguous 7-ha compartments.[4] The four regimes were (1) two heavy thinnings at 9-year intervals, (2) three medium thinnings at 6-year intervals, (3) six light thinnings at 3-year intervals, and (4) no thinning (Fig. 1). Initial thinning removed 16-42% of the basal area. After the second thinning on the 3-year cycle, differences in relative basal area among the three thinned stands were always less than differences between thinned and unthinned stands. Last thinnings were in 1957, 1960, and 1963, respectively, on the 9-, 6-, and 3-year cycles.

Methods

Basic study (1950-1971)

Amount and timing of annual seedfall was determined by the use of seed traps (Fig. 2). Each trap had a 61- by 91-cm top surface which caught the seed and litter which fell on this 0.56-m^2 area. Ten traps were placed in each of the four treatment compartments. To eliminate bias, each trap was placed 3 m north of a randomly selected plot center. Collections were made five times a year; approximately, October 2, October 23, December 12, April 6, and August 18. Traps were set out in August 1950. Subsequent August collections marked the end of collections for the foregoing seed year and the start of the collection period for seed dissemination from the current crop of cones.

On each collection date, the content of each trap was placed in a paper sack. After drying, Douglas-fir seeds were sorted from the litter and the total number tallied. Seeds were then cut with a razor blade to determine whether they were filled. Squirrel activity complicated determination of seed production because seeds dropped from cones which they tore apart, either on or above the traps, were distributed unevenly. Such seeds were often a substantial part of the total catch. Adjustments for these occurrences excluded the excessive count from any trap on which cone remains were present; instead the average seed count from other traps in the same treatment and date was assigned. Seeds hulled by rodents are included with filled seeds in this report.

Only one replication of the treatments was measured during the period 1950-1971. The 10 traps existing within each treatment do not provide a basis for estimating an experimental error. Thus, no statistical tests were performed.

Supplemental study (1972-1978)

In August 1972, 32 of the seed traps were moved to different locations, scattered over the entire thinning trial, in conjunction with another study. Collections from these traps were made only three times a year, but otherwise collection and counting procedures were the same as described for the basic study. Seed production estimated from the average seed catch in these traps has been included in this paper to extend the information on size and periodicity of seed crops, proportion of seed filled, and seasonal dissemination of seed. The author believes this 7-year record is suitable for these purposes, even though not completely compatible with the 22-year record from the basic study reported here.

Results and discussion

Size and periodicity of seed crops

During the 29 years of record, total annual seedfall ranged from zero to nearly 2.5 million seeds per hectare in the unthinned sand and to more than 3.1 million seeds per hectare in one thinned stand (Fig. 3).[5]

Crops of more than 100 000 filled seeds per hectare were produced in 7 years in both unthinned and thinned stands, and in 2 additional years, 1950 and 1965, in thinned stands. The latter six of these nine crops occurred at 1- to 4-year intervals. The other 20 crops all produced fewer than 50 000 filled seeds per hectare, with an average of only about 7000.

Three crops of more than 450 000 filled seeds per hectare were produced at 5- to 6-year intervals, in 1959,

[4] The entire thinning trial included three replications of these four regimes, in a randomized block design (Reukema 1972). The basic seedfall study (1970-1971) was confined to one replication (block) of the thinning trial, which is described here.

[5] The figures and tables included in this paper highlight major points on which the author wishes to focus attention. For readers desiring more detail, comprehensive tables are on file at the Forestry Sciences Laboratory, Olympia, WA.

FIG. 2. Seed trap used in the study with top raised for better viewing. (In use, the top rests flat on the bottom portion and is held in place by the pegs at diagonally opposite corners.)

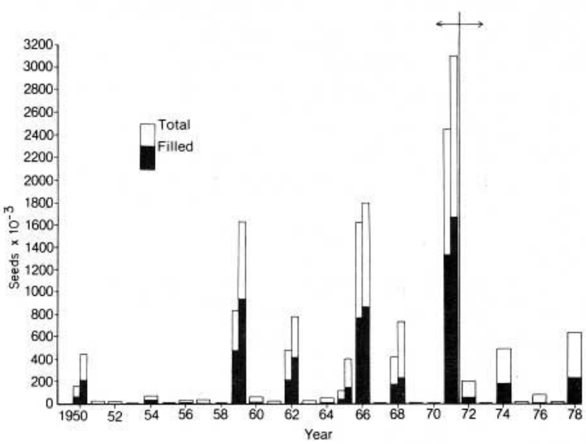

FIG. 3. Annual total and filled seeds per hectare. Both unthinned and best thinned are shown for 7 years to illustrate extremes; for other years, when treatment had little effect on seed production, averages of all treatments are shown.

1966, and 1971. The 1971 crop was by far the largest, with about 1.5 million filled seeds per hectare. Regional cone-crop reports (Anonymous 1954-1969; Anonymous 1970-1978) indicate that these three best crops correspond to the only years in which there was generally a good cone crop throughout the region; again, in general, 1971 was best. Thus, the apparent trend of increasing crop size among the three largest crops with increasing stand age was likely due in large part to year-to-year variation. The other six larger crops, 1950, 1962, 1965, 1968, 1974, and 1978, correspond to years in which crops were generally poor, but spotty, throughout the region. A bumper crop had been forecast for 1978 but did not materialize because cone development was impaired by late spring frosts accompanied by east winds. Some areas within the region did produce a very good crop.

The periodicity shown in this study is consistent with what others have observed. Isaac (1943) observed that the time between abundant cone crops averaged about 5 years, and varied from 2 to 11 (or more). Allen and Owens (1972) reported abundant or medium cone crops occur every 2 to 7 years, and commonly about every 5 years.

Proportion of seeds filled

The proportion of seeds which were filled was related to size of seed crop ($R^2 = 0.425$), but varied substantially. This proportion ranged from 44 to 54% for the 3 best crops; 30 to 48% for the next 16 best; and less than 20% for the 15 poorest crops.

The proportion of seeds filled also varied with time of seedfall, generally declining as the season progressed (Fig. 4). In all of the 9 best years, this proportion declined quite rapidly after the December collection. The early season pattern was more variable; in some

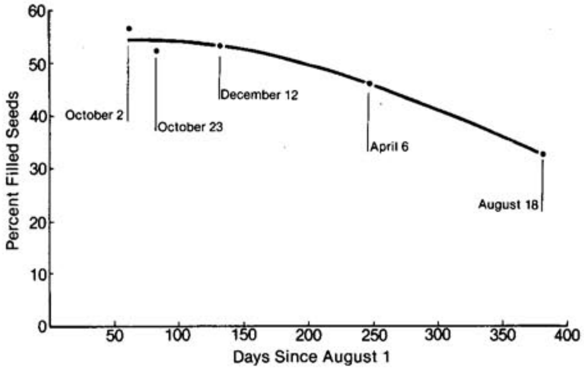

FIG. 4. Average proportion of seeds filled, by collection date.

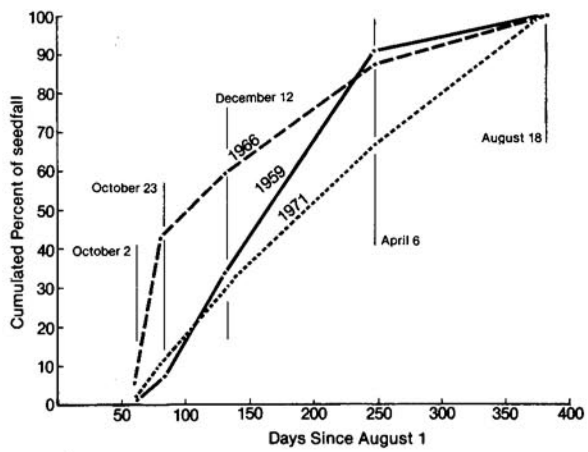

FIG. 5. Seasonal distribution of seedfall in the three best crop years; average of all treatments.

years it peaked at the late October collection, whereas in other years it was highest at the October 2 collection. The decline in the latter part of the season agreed with Garman's (1951) observations.

Thinning generally had no effect on the proportion of seeds filled. Substantial variation among treatments in some years was erratic and apparently happenstance. A relatively high proportion of seeds filled in the heavily thinned stand in 1950 may be an exception to this generality.

Seasonal dissemination of seed

Typically, one third to one-half of the seed was shed by late October, about two-thirds by mid-December, and more than 90% by early April. For filled seed only, commonly about half fell by late October and threefourths by mid-December. There was considerable year-to-year variation, however.

For two of the three largest crops, dissemination of seed was substantially delayed (Fig. 5). For both 1959 and 1971 crops, only about one-third of the seed had fallen by mid-December. For the 1971 crop, a third of the seed did not fall until after early April; this included more than 20% of the filled seed.

This delayed dissemination in 1959 and 1971 suggests that dissemination may be spread over a longer period when seed crops are large. Dissemination of seed from the large 1966 crop, however, closely followed the typical pattern. Also, for years in which seed crops were much larger in thinned than in unthinned stands, timing of dissemination did not differ between stands. Thus, weather conditions undoubtedly have a stronger influence on timing of dissemination of Douglas-fir seed than does size of crop. Isaac (1943) noted that the period of dissemination could vary greatly according to the occurrence of dry or wet weather. Whereas he reported that typically two-thirds of the seed was shed by the end of October, in Oregon and Washington, both Pickford (1929) and Garman (1951) observed that only about half the seed fell by the end of October and about two-thirds fell after the 1st of March, in British Columbia.

TABLE 1. Total seedfall, by treatment and year

Year	Thinning cycle (years)*				Average % filled
	None	3	6	9	
1950	161	135	108	447	37
1959	827	1458	1405	1629	54
1962	470	678	743	782	48
1965	113	434	341	396	30
1966	1620	1354	1319	1805	44
1968	423	527	448	746	32
1971	2461	2443	2474	3112	51

*Values given in thousands of seed per hectare.

Effects of thinning

Thinning had little effect on either the proportion of seeds filled or timing of seed dissemination. Both were very consistent among treatments in all years. Likewise, thinning generally had little effect on the amount of seed produced in poor seed years. It did, however, have a substantial effect on the amount of seed produced in some of the better seed years. Apparent effects of thinning on seed production are described for the seven best crops which occurred during the 22 years of record, 1950-1971 (Table 1).

Seed production in 1950 was apparently improved by heavy thinning (9-year cycle) made in 1948. Whereas, the stand thinned on the 9-year cycle always produced more seed than other thinned stands, the relative difference in 1950 was much greater than in any other year. This heavily thinned stand produced nearly three times as much seed as the unthinned stand. Failure of the initial light and moderate thinning to stimulate production of seed in 1950 may be associated with timing of the thinning. Bud primordia for the 1950 cone crop were formed in the spring of 1949 (Allen and Owens 1972). Thinning in the heavily thinned stand had been completed prior to that, whereas thinnings in the moderately and lightly thinned stands were not completed until October 1949 and March 1950, respectively.

In subsequent years, the stand thinned heavily on a 9-year cycle produced 23% more seed than the average of the other thinned stands. It is not clear to what extent this is an effect of being thinned differently from the other stands, as thinning cycle is confounded with location. If attention is focused on comparison between the other thinned stands (3- and 6-year cycles) and the unthinned stand, clear trends over time are evident.

Thinning on 3- and 6-year cycles apparently resulted in substantially improved seed production in 3 years, 1959, 1962, and 1965. These three crops occurred 2 to 5 years after most recent thinnings, and I 1 to 17 years after initial thinnings. In the good 1959 seed year, these thinned stands produced about 75% more seed than the unthinned stand. In 1962, the apparent gain from thinning was less, but still very substantial. In both of these years there was an apparent inverse relationship between seed production and relative stocking level, as seen by comparing Table I and Fig. 1.[6] In 1965, the poorest crop on which thinning had an effect, thinned stands produced more than three times as much seed as the unthinned stand. Such stimulation of seed production by thinning is consistent with observations elsewhere (Puritch 1972).

The contrast between effects of past thinning on seed production in 1965 and 1966 is striking. In 1966, the largest crop to that date, stands which had been thinned on 3- and 6-year cycles produced less seed than the unthinned stand. It might be appropriate to consider the 1965 and 1966 seed crops as a single crop. Relative seed production in these consecutive years was probably influenced by environmental conditions which affected timing of cone production, as opposed to increasing total production as in prior years. These conditions apparently triggered part of the crop to be produced a year earlier than the main crop, more so in the thinned stands than in the unthinned stand; 18 to 24% of the 1965-1966 total was produced in 1965 in thinned stands versus 6.5% in the unthinned stand. Many trees which produced good cone crops in 1965 probably did not do so in 1966 (Owens 1969). Combined seedfall for the 2 years was virtually the same for stands thinned on 3- and 6-year cycles as for the unthinned stand.

The effect of past thinning had apparently worn-off before completion of the final thinning cycle in 1966. Again in 1968 and with the bumper crop in 1971, seed production was similar in thinned (3- and 6-year cycles) and unthinned stands, even though thinned stands still had low stocking levels.

The apparent decreasing effect, over time, of stocking level on seed production may be related to either stand age or time since initial thinning, or both. These possibilities cannot be separated. Recency of subsequent thinnings apparently had little effect on seed production, however. Furthermore, the effect of stand density may be confounded with other factors affecting seed production. In some years, much better seed crops are produced in open stands than in closed stands; whereas in other years, both open and closed stands produce good crops (Issac 1943).

Conclusions and implications

This unique long-term record of seedfall, at a single location in western Washington, supports accepted generalizations regarding periodicity of seed crops and timing of seed dissemination. It quantifies the size of seed crops which may be produced by young Douglas-fir stands, and provides information regarding effects of thinning thereon. It should be indicative of crops likely to occur in other young Douglas-fir stands, but inferences from this study are limited by the single location and lack of replication of thinning treatments.

Between ages 48 and 67 (1959-1978), crops judged adequate for natural regeneration were produced at 1- to 4-year intervals. Thus, such stands, which are younger than conventional harvest age, could frequently be depended on to naturally regenerate adjacent clear-cuts or under a shelterwood cut. Typically, one-third to onehalf of the seeds were shed by late October and about two-thirds by mid-December. Few were shed before the first of October or after the first of April. For two of the three best crops, shedding of much of the seed was greatly delayed; but an ample supply was on the ground when conditions were favorable for germination.

Thinning generally had no effect on the amount of seed produced in years when the unthinned stand produced a poor crop. The greater seed production in thinned stands in 1950 and 1965 may be minor exceptions to this generality. The greater production in thinned stands in 1965 was apparently at the expense of part of the good 1966 crop but resulted in two adequate consecutive crops. Likewise, thinning had no apparent effect on either the proportion of seeds filled or the timing of seed dissemination.

Thinning clearly did stimulate increased seed production in 1959 and 1962 and apparently caused many

[6] This relationship could not be realistically quantified with the data available because (1) sampling procedures may not have provided comparable estimates for the two variables, and (2) there were substantial pretreatment differences in estimated stocking levels.

trees to produce a crop in 1965, a year earlier than they would have otherwise. It apparently stimulated seed production in 1950. Much of the increase in amount of seed owing to thinning may be surplus to needs for natural regeneration, but would be of major importance for collection in seed production areas. Unfortunately, the relationship between seed production and thinning intensity could not be quantified but it appears that favoring selected trees by removal of about one-third of the basal area in trees surrounding them would increase seed production in the next adequate year by at least 50%, and probably more.

The beneficial effect of past thinning on seed production did not last, however, even though stocking level remained much lower in the thinned than in the unthinned stands. This probably indicates that openness of the stand has less impact on seed production as the stand becomes older, or with increasing time since initial thinning. It appears that frequent thinnings, after the initial thinning, will not maintain improved seed production, at least over a prolonged period.

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