

Estimating seed crops of conifer and hardwood species

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Cone, acorn, and berry crops of ponderosa pine (*Pinus ponderosa* Dougl. ex Laws. var. *ponderosa*), sugar pine (*Pinus lambertiana* Dougl.), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), California white fir (*Abies concolor* var. *lowiana* (Gord.) Lemm.), incense-cedar (*Libocedrus decurrens* Torr.), California black oak (*Quercus kelloggii* Newb.), tan oak (*Lithocarpus densiflorus* (Hook. & Arn.) Rehd.), and Pacific madrone (*Arbutus menziesii* Pursh) were evaluated over a 24-year period (1958–1981) from an area in northern California by an easy to use visual crop rating system. Seed-trap data, also for 24 years, were gathered for four conifer species. Together, these data provide the wild-land manager with knowledge on seed-crop quantity, quality, and timing. The visual rating system involves visually estimating the amount of fruit in trees and the proportion of trees with fruit, and ranking the crop by species. Regressions of sound seed and total seed on seed-crop rating are provided for the two species with the most seed crops: ponderosa pine and Douglas-fir. Regressions were significant at the 1% level, and coefficients of determination ranged from 0.58 to 0.76.

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La production de cônes, de glands et de baies a été évaluée à l'aide d'un système visuel et facile à utiliser d'estimation de la production semencière et ce, pendant 24 ans (1958–1981), dans une aire du nord de la Californie, chez le pin à bois lourd (*Pinus ponderosa* Dougl. ex Laws. var. *ponderosa*), le pin à sucre (*Pinus lambertiana* Dougl.), le sapin de Douglas (*Pseudotsuga menziesii* (Mirb.) Franco), le sapin «du Colorado» (*Abies concolor* var. *lowiana* (Gord.) Lemm.), le cèdre à encens (*Libocedrus decurrens* Torr.), le chêne noir de Californie (*Quercus kelloggii* Newb.), la pasanie densiflore (*Lithocarpus densiflorus* (Hook. & Arn.) Rehd.) et l'arbousier du Pacifique (*Arbutus menziesii* Pursh). Des données de piégeage des semences ont aussi été prises pendant la période de 24 ans pour quatre espèces conifériennes. L'ensemble de ces données donnent à l'aménagiste du territoire naturel des connaissances au sujet de la qualité, la quantité et la maturation des productions semencières. Le système visuel d'estimation implique d'évaluer visuellement la quantité de fruits dans les arbres et la proportion d'arbres avec des fruits, ainsi que d'ordonner la production semencière par espèce. Des régressions de la quantité de semences saines et de la quantité totale de semences sur l'estimation de la production semencière sont présentées pour les deux espèces ayant le plus de productions semencières : le pin à bois lourd et le sapin de Douglas. Les régressions étaient significatives au seuil de 1% et les coefficients de détermination variaient de 0,58 à 0,76.

[Traduit par la rédaction]

Introduction

Seed production and its quantity, quality, and timing are of increasing interest to wild-land managers, especially those concerned with biodiversity and maintenance of ecosystems. To the forest ecologist, seed crops and their periodicity give knowledge on future plant and animal populations and the diversity of species in related communities. To the wildlife biologist, amount of seed can mean the difference between healthy and unhealthy animals and even high and low population levels. And to the extent that plantings will be used to restore damaged ecosystems, as well as to provide future timber crops, timing and size of seed crops are of particular importance to forest regeneration specialists because they form the basis for the gathering of fruit and the magnitude of many nursery operations.

Quantifying and rating cone crops in California is not new. Fowells and Schubert (1956) studied seed production of several California conifers, with emphasis on ponderosa pine (*Pinus ponderosa* Dougl. ex Laws. var. *ponderosa*), sugar pine (*Pinus lambertiana* Dougl.), and California white fir (*Abies concolor* var. *lowiana* (Gord.) Lemm.) in central California. They laboriously counted cones, caught seed in seed traps, and developed a relationship between number of seeds per acre and number of cones per acre. From 1958 through at least 1965, the cone crops of 19 to 26 conifer species in California were rated annually by a visual system (Schubert 1958; Eden 1965). However, no check on the accuracy of the rating system or its relationship to the quantity or soundness of seeds was done.

This paper describes a relatively quick and easy to use system for rating seed crops of the major conifer and hardwood species in the northern Sierra Nevada, and evaluates the worth of the system, at least for conifers, by checking it with seed-trap data. This paper also provides wild-land managers with information on the proportion of sound seed by species, and the timing and magnitude of seed crops on high sites, that can help them draw inferences about the future regeneration of individual species or mixtures of species.

Methods

Site and stand

This study took place on the Challenge Experimental Forest and surrounding area in central northern California, 42 km northeast of Oroville. An important attribute of the experimental forest is its high site quality. Dominant and codominant ponderosa pines average 34 m in 50 years (Powers and Oliver 1978). Soils often are more than 9 m deep (as seen in road cuts), mean annual temperature is 13°C, and annual precipitation averages 1680 mm. Frost-free days average about 190 each year.

In stand volume, ponderosa pine is the dominant species, followed by Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), with lesser amounts of sugar pine, California white fir, and incense-cedar (*Libocedrus decurrens* Torr.). Hardwoods, principally California black oak (*Quercus kelloggii* Newb.), tan oak (*Lithocarpus densiflorus* (Hook. & Arn.) Rehd.), and Pacific madrone (*Arbutus menziesii* Pursh), are scattered throughout as individual trees, clumps, or groves. Average stand density in conifer and hardwood trees larger than 8.9 cm DBH is 613 trees/ha. Basal area averages 62 m²/ha. The

forest is made up of a mosaic of even-aged stands, depending on fire history, with the oldest dominant and codominant trees being about 120 years old. In general, many trees of the more shade tolerant species (Douglas-fir, California white fir, incense-cedar, and tan oak) are of younger age-classes, reflecting a decreasing incidence of fire in the area.

Measurements and analysis

Seed crops of conifers and hardwoods were evaluated between late summer and late fall from 1958 through 1981. Because cones, berries, and acorns do not mature at the same time each year, we began to closely observe the seed crops of the various species in late summer. Seed crops of each species were rated two or three times per week during that period (usually about 2 weeks) when the fruit of individual species were judged to be fully developed, most easily seen, and at or near maximum number. Binoculars (6 × 30) were used each year. Scores of trees in many stands were observed each day, although the same trees were not checked each year.

Size of seed crops, whether cones, berries, or acorns, was estimated visually on trees larger than 13 cm DBH, and the crops were placed in categories. These estimates, gathered during the 2-week period, then were pooled to give an overall rating for each species each year:

Category	Description
(0) Minimal	No fruit or a few fruit on less than 5% of trees
(1) Very light	Few fruit on less than 25% of trees
(2) Light	Few fruit on more than 25% of trees
(3) Medium	Many fruit on 25 to 50% of trees
(4) Heavy	Many fruit on more than 50% of trees

In this instance, the terms few and many related to a heavy seed crop; heavy being the crop size most easily conceptualized by crop evaluators. Consequently, few was less than 50% of a heavy crop, and many was 50% or more.

Rating the proportion of trees with a certain amount of fruit helps define the size of a seed crop, but still needed is a check on the rating system. This is gained by assessing the relationship between total seed and seed-crop rating by regression.

Seed traps were about 0.3 by 0.3 m. They were made of galvanized wire screen, with openings in the top mesh being about 0.6 cm. This orifice did not permit reliable sampling of sugar pine seeds or fruits of hardwood species. For smaller seeded species in this study, the reliability of this size of trap has been ascertained (McDonald 1973; Roy 1959). Estimates of seedfall were based on seed traps located in three compartments (areal subdivisions of the experimental forest), which were fully stocked and representative of the species composition and stand structure there and in the surrounding area. However, because the compartments did not constitute replications, it was not possible to estimate an experimental error for testing compartment differences.

In each compartment seed traps were arranged along transects that numbered three to nine per compartment. Transects were randomly chosen, and seed traps were systematically laid out along them. Sampling intensity was six traps per transect, for a total of 108 traps in the study. Collections from the traps were made in late fall or early winter after most seeds had been disseminated, and again in the subsequent August, when winter- and spring-fallen seeds were collected. Seed from these two collections made up the sample for the foregoing seed year. Contents of each trap were placed in paper sacks. After drying, seeds were sorted from the litter and the total number was tallied. A cutting test determined seed soundness. Both sound and unsound seeds were calculated on a per hectare and per compartment basis, and averaged over the three compartments.

Applicability of the seed-crop rating system was ascertained by regressions (SAS Institute Inc. 1988) of total seed crop on seed-crop rating for the two species with the most seed crops: ponderosa pine and Douglas-fir.

Results and discussion

Because of the high quality of the site, the potential for both frequent and large seed crops is high. Production, however, tends to be variable. Some dominant seed trees produce many cones every 3rd or 4th year; others nearby produce none. Sundahl (1971) noted that the presence of cones at the base of a tree is a key selection criterion for ponderosa pine seed trees in the study area. Linhart (1988) noted that within a ponderosa pine stand, about 20% of the trees produce 70 to 80% of the cones and are major contributors to cone crops year after year. Age of tree, size of crown, position in stand, degree of flowering, success of pollination and fertilization, interplay of high and low temperatures during early seed development, and damage by insects all play major roles in the size and timing of seed crops. Consequently, the production of seed is at best an uncertain process. And determining the soundness of seed in cones and berries and of acorns in standing trees is extremely difficult.

Periodicity and size of seed crops

During the 24-year period, the five conifer species produced 51 seed crops, ranging from very light to heavy. The number of crops by species and category were as follows:

	Medium-heavy	Very light – light	Total
Ponderosa pine	7	7	14
Douglas-fir	2	11	13
California white fir	5	1	6
Incense-cedar	1	9	10
Sugar pine	2	6	8

Ponderosa pine and California white fir produced the most medium to heavy seed crops; Douglas-fir, incense-cedar, and sugar pine tended to put forth light or very light seed crops. California white fir was unique in that it tended to produce either medium seed crops or virtually none at all (Fig. 1). Of particular note was that conifer species tended to produce medium to heavy seed crops in similar years. Years of poor or absent crops also tended to coincide.

The three hardwood species produced 30 seed crops during the 24-year study period. Seed-crop rating (number of crops) by species was as follows:

	Medium-heavy	Very light – light	Total
California black oak	3	2	5
Tan oak	4	9	13
Pacific madrone	2	10	12

Although each hardwood species put forth about the same number of medium to heavy seed crops, the tendency for tan oak and madrone was to produce many light and very light crops. Unlike the conifers, the hardwood species produced crops in no discernible pattern (Fig. 2). Only in one year, 1975, did more than one species produce at least a medium crop. And only in two years did a medium to heavy crop of acorns or berries coincide with a medium or heavy crop of cones.

Estimates of conifer seed production from seed traps ranged from none to 760 000 sound seeds/ha and from none to 520 000 unsound seeds/ha in a given year (Fig. 3). The

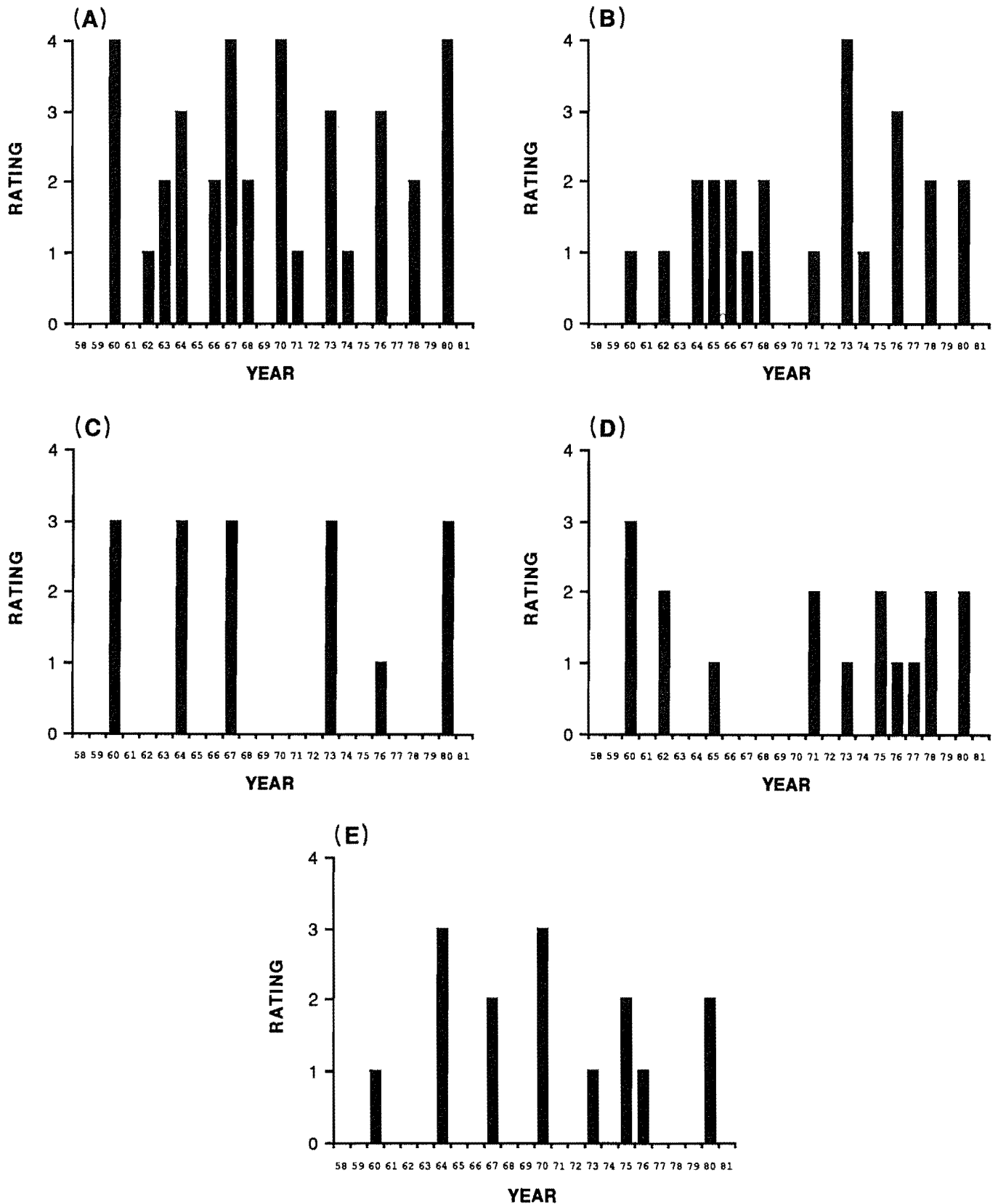


FIG. 1. Annual rating of cone crops at Challenge Experimental Forest, 1958–1981. (A) Ponderosa pine. (B) Douglas-fir. (C) California white fir. (D) Incense-cedar. (E) Sugar pine.

TABLE 1. Statistics for ponderosa pine and Douglas-fir seed (from seed traps) relative to values in the rating system

Rating	Parameter	Ponderosa pine		Douglas-fir	
		Sample size (no. of years)	No. of seeds/ha ^a	Sample size (no. of years)	No. of seeds/ha ^a
0	Mean	10	2790	11	3353
	Range		0 – 17 942		0 – 20 929
	CI ^b		0–6158		0–7003
1	Mean	3	33 976	5	23 146
	Range		3655 – 76 420		8639 – 47 181
	CI ^b		0 – 97 817		9120 – 37 173
2	Mean	4	55 316	6	30 070
	Range		26 244 – 95 677		17 608 – 41 204
	CI ^b		21 112 – 89 522		21 369 – 38 772
3	Mean	3	331 146	1	232 573
	Range		210 986 – 457 839		—
	CI ^b		129 980 – 532 310		—
4	Mean	4	737 705	1	351 507
	Range		402 674 – 1 275 683		—
	CI ^b		293 829 – 1 181 583		—

^aSound and unsound seed combined.^bThe 95% confidence interval.

highest annual seedfall occurred in 1980. Ponderosa pine, which represented 67% of all conifers more than 41 cm DBH, produced the top seven seed crops and 90% of the sound seed produced during the 24-year study period.

Estimates of seed production for hardwoods on the experimental forest are scant, but a few are available. Sampling by temporary 4-m² plots during the heavy tan oak seed year of 1974 revealed that there were an average of between 220 000 and 420 000 sound acorns/ha (McDonald 1978). On a tree basis, beneath a clump of four tan oak trees that were 25, 33, 36, and 36 cm DBH, were an average of 870 000 sound acorns/ha. Number of Pacific madrone berries on three trees, during the very light seed year of 1976, averaged 49 000 per tree, with a range of 13 000 to 108 000 per tree. Number of seeds per berry ranged from 2 to 37, averaging about 20.

Percentage of sound seed

In general, percentage of sound seed in conifers tended to be low when number of cones was low and higher as number of cones increased. Most often, the percentage of unsound seed was higher than that of sound seed, with the exception being ponderosa pine and California white fir in 1970, and ponderosa pine and incense-cedar in 1980. In absolute terms, however, the largest amount of unsound seed was disseminated in medium and heavy seed years.

For medium to heavy seed crops, percentage of sound seed by species was as follows:

	Average (%)	Number	Range (%)
Ponderosa pine	43	7	31–59
Douglas-fir	11	2	9–13
California white fir	20	5	11–33
Incense-cedar	50	1	

Of particular interest was the strong relationship of sound ponderosa pine seed to seed-crop rating: as seed-crop rating increased, the percentage of sound seed increased (Fig. 4).

The most representative equation relating these variables was $y = a + bx$; where y is percentage of sound seed and x is seed-crop rating. The best least-squares expression of this relationship was percentage of sound seed = $-1.009 + 11.464$ rating. The regression was significant at the 1% level. The standard error of regression was 8.52, and the coefficient of determination was 0.83.

No relationship between percentage of sound seed and rating for Douglas-fir was found. An increase in the seed crop did not result in an increase in the percentage of sound seed, which tended to be low throughout the 24-year study period.

Soundness of specific hardwood seed crops usually is based on periodic examination of acorns on the ground. Although not ascertained for each crop each year, some estimates of soundness were noted in diaries based on acorns gathered for propagation purposes. Acorns in the heavy tan oak crop of 1969, for example, were 73% sound; those in the light crop of 1971 were 50% sound. Acorns in the medium crop of 1975 were almost all wormy, not surprising because the previous year's crop was heavy and the population of insect predators was high.

Applicability of rating system

Potential users of a seed-crop rating system want to know the relationship between total seedfall and the rating system.

In this study, mean total seeds per hectare for each numerical rating and width of confidence band increased as numbers in the rating system increased (Table 1). Sound seed and total seed were plotted against seed-crop ratings for ponderosa pine and Douglas-fir. The relationship was tentatively expressed in several mathematical equations (SAS Institute Inc. 1988). The most representative equation relating seedfall to rating was $\ln(y + 1) = a + b \ln(x + 1)$; where $y + 1$ is total seedfall and $x + 1$ is seed-crop rating. The terms $\ln(y + 1)$ and $\ln(x + 1)$ were necessary to avoid the $\ln(0)$ problem. The best expressions of this relationship for both ponderosa pine and Douglas-fir are given in Table 2.

Comparing the annual ratings of the conifer species in Fig. 1 with the corresponding seed production data in Fig. 3 shows some strengths and weaknesses of the seed-crop rating

TABLE 2. Equations relating seedfall to crop rating for ponderosa pine and Douglas-fir

	Seed crop	Equation	R^2	P-value	SE of regression
Ponderosa pine	Sound	$\text{Ln}(y + 1) = 0.55 + 7.26 \ln(x + 1)$	0.76	<0.01	2.81
	Total	$\text{Ln}(y + 1) = 3.02 + 6.94 \ln(x + 1)$	0.72	<0.01	2.93
Douglas-fir	Sound	$\text{Ln}(y + 1) = 0.79 + 6.02 \ln(x + 1)$	0.61	<0.01	2.73
	Total	$\text{Ln}(y + 1) = 3.54 + 6.60 \ln(x + 1)$	0.58	<0.01	3.17

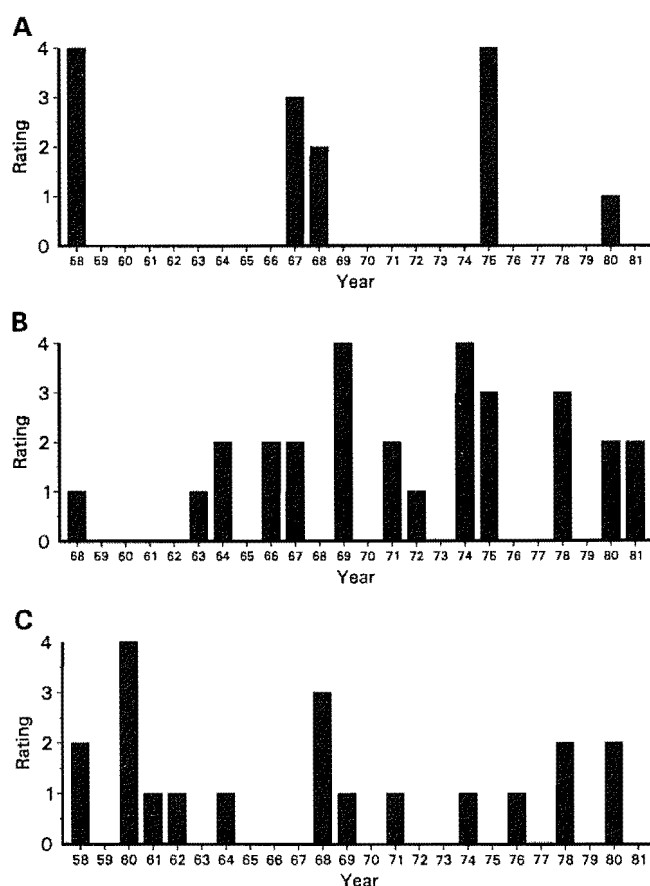


FIG. 2. Annual rating of hardwood seed crops at Challenge Experimental Forest, 1958–1981. (A) California black oak. (B) Tan oak. (C) Pacific madrone.

system. In general, the system worked well for ponderosa pine, whose sound-seed production increased in proportion with total seed production. It also well portrayed the seed crops of California white fir, a species that produced mostly medium seed crops and few light ones. For species like Douglas-fir and incense-cedar, which tend to produce mostly light or very light crops, the system generally identified the medium and heavy crops, but did not differentiate very well between light and very light crops. This discrepancy probably relates to the difficulty of observing small cones on tall trees and indicates a need for extra care when estimating small cone crops of these species.

Although acorn and berry crops were not checked in seed traps in this study, visual seed-crop rating systems, similar in principle but differing in technique from that used in this paper, have been used to evaluate crops of several native

California hardwoods, including California black oak (Carmen *et al.* 1987; Graves 1980). These systems have been deemed practical, and the data and trend information have been used to monitor acorn production throughout California, and to provide estimates of food for wildlife (McKibben and Graves 1987).

Seasonal dissemination of seed

For conifer species, the first seeds to fall usually were those of Douglas-fir, followed by incense-cedar and ponderosa pine, and then by sugar pine and California white fir. The diary of 1980 presents typical weather and timing of seedfall on the experimental forest. Unsound seeds of Douglas-fir and incense-cedar were first noticed on August 12, with sound seed of Douglas-fir beginning to fall by September 12 and that of incense-cedar by September 15. Ponderosa pine began producing sound seed by October 12, and sugar pine and California white fir by October 10. By October 15, seed was falling from cones of all species. Hot, dry weather, particularly with northeast winds, enhanced seedfall. Storm winds from the southwest, typically with higher humidity, tended to decrease seedfall.

Diary records in other years indicated that October generally is the month when seedfall of conifers is greatest. Rarely were sound seeds found when the seed traps were emptied the following August, indicating that almost all seeds had fallen by early winter. Most seeds fell during a northeast wind, a fact verified in a study on the forest, which showed that natural regeneration was best in the northeast quadrant of circular clear-cuttings and extended in a pie-shaped wedge to near the clear-cutting center (McDonald 1983).

Fully developed California black oak acorns were first noted on the ground about September 1, when brown, yellowish brown, and greenish yellow acorns fell. Most showed evidence of attack by lepidopterous and coleopterous insects, which can destroy up to 95% of an acorn crop (Keen 1958). Some mostly brown acorns had a white moldy ring around the scar at the rounded end of the acorn. Cut acorns revealed that this ring was a good indicator of moldy interiors or insect-attacked and moldy interiors. Fall of sound acorns consistently began about October 15, peaked in 12 to 15 days, and tapered off rapidly. By mid-November acorn fall had ceased. This schedule was applicable if October generally was warm and dry with northeast winds. Storms from the southwest tended to prolong the period of acorn fall.

Timing of acorn fall for tan oak was similar to that of California black oak. September to mid-October was the time for aborted, insect-attacked, and healthy-appearing green acorns to fall. Peak fall occurred around October 20, particularly if warm, dry, northeast winds were blowing. Acorn fall generally ceased by November 15.

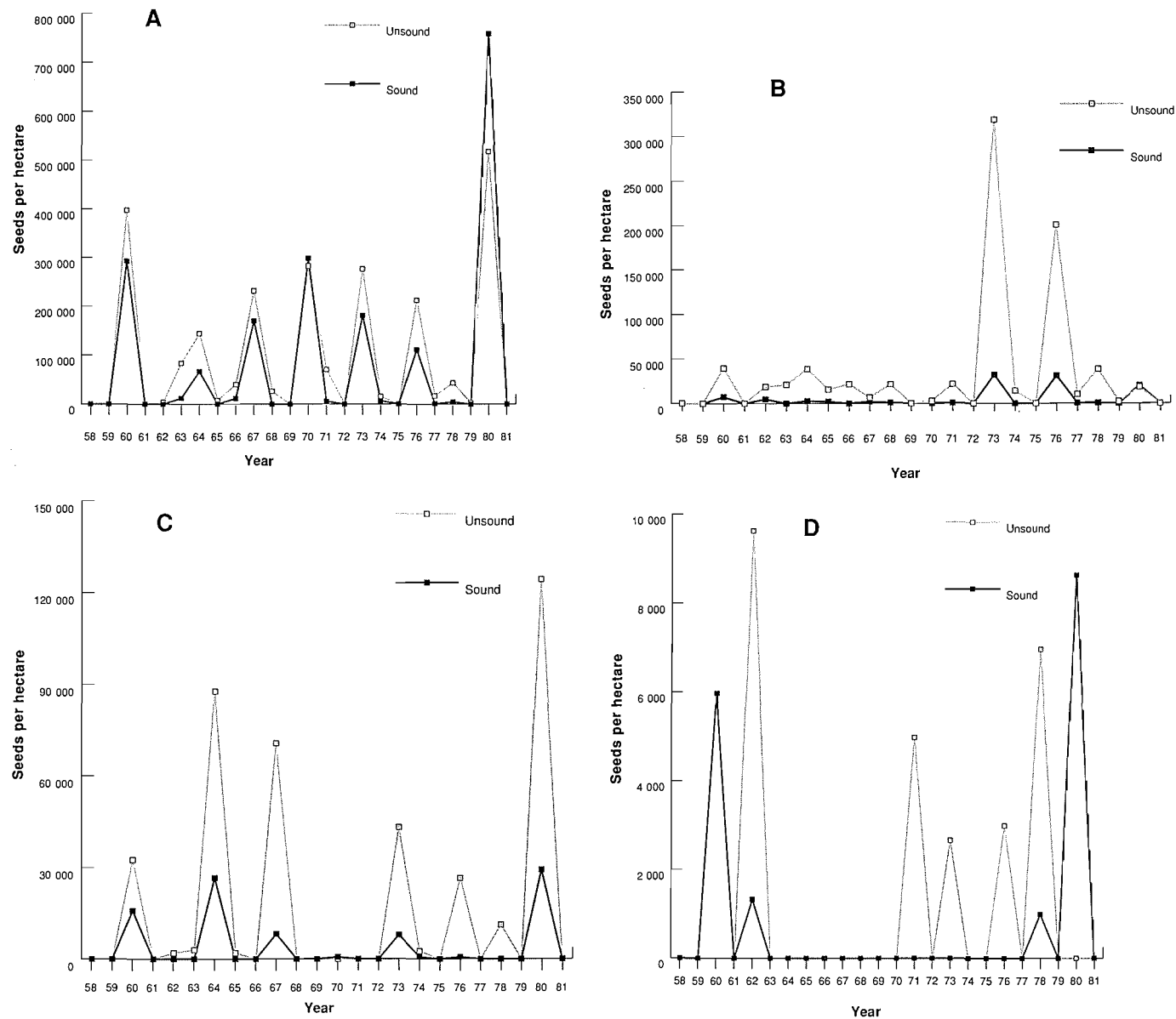


FIG. 3. Seed production at Challenge Experimental Forest, 1958–1981. (A) Ponderosa pine. (B) Douglas-fir. (C) California white fir. (D) Incense-cedar.

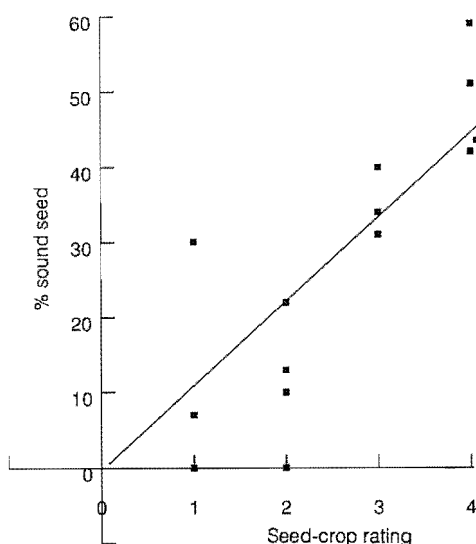


FIG. 4. Relationship of sound seed to seed-crop rating for ponderosa pine.

Berries of Pacific madrone mature from mid-September to mid-October. Ripe berries are bright red or reddish orange, but a given cluster may also contain berries that are yellowish orange or even yellowish green at maturity. The berries are disseminated by gravity and a host of consumers, particularly the mourning dove (*Zenaidura macroura*) and the band-tailed pigeon (*Columba fasciata*). Often, the length of time that berries remain in the trees depends on the degree of consumption by these birds. In several years, berries were gathered from newly fallen trees in mid-January or near the end of January. Those gathered near the end of the month were noted as being small and shrivelled. In other years, berries were gone from the trees by mid-December.

Conclusions and implications

This long-term record of seedfall, from an area in the northern Sierra Nevada of California, rated the cone, acorn, and berry crops of five conifer and three hardwood species, and quantified on the ground seedfall for several species. Findings should be indicative of the frequency and magnitude of crops likely to occur in other young-growth, mixed conifer, and hardwood stands on good sites. Although the method for estimating seed crops may have utility elsewhere, inferences on the magnitude and periodicity of seed crops are limited by the single location and lack of statistical reliability of the seed-trap estimates.

For 120-year-old ponderosa pines and younger, more shade tolerant conifers and hardwoods, 51 conifer and 30 hardwood seed crops were produced in a 24-year period (1958–1981). Of these, 17 conifer and 9 hardwood crops rated medium to heavy. A notable feature of cone, acorn, and berry production was consistency in the timing of crops. The seven medium to heavy crops of ponderosa pine occurred every 3 or 4 years, those of California white fir occurred every 5 years, and those of California black oak occurred every 8.5 years. Rare was the year that no seed was produced by a conifer or hardwood

species, and common was the year that at least three species of conifers produced at least some seed. Little synchrony existed between conifer and hardwood crops.

Another worthwhile finding of this study was the relatively high proportion of unsound seed. With only a few exceptions, seed crops of the four conifer species were less than 50% sound. This finding may be characteristic of not-yet mature trees and useful when determining the number of seeds that will be needed to produce an acceptable crop of natural seedlings.

Wild-land managers, including foresters, ecologists, wildlife biologists, and others, often need to know the amount of seed that will be falling from various species over time. The seed-crop rating system tested in this paper gives them a handy means of estimating seed-crop size.

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