

CONE AND SEED PRODUCTION IN *PINUS PONDEROSA*: A REVIEW

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ABSTRACT.—Factors associated with seed cone production in *Pinus ponderosa* were reviewed to identify broad patterns and potential effectiveness of restoration activities. Cone and seed production are quite variable, with differences between (1) years, (2) sites, and (3) individual trees. Between-year, population-wide crop failures suggest large-scale triggers for cone and seed production, perhaps high temperatures and dry weather. Stem diameter is the most important determinant for cone production at the tree level, with other factors such as genetic disposition, moisture, soil nutrients, and insect pests and disease playing a smaller role. Some extrinsic factors affect growth rate, indirectly affecting cone production. For example, less competition and lower stand densities result in *P. ponderosa* trees that increase in diameter more quickly, possibly because of more light, and produce seeds earlier. This literature suggests that restoration activities, especially thinning, will result in trees better able to produce larger seed crops. The effect of prescribed fire is less clear, with contradictory effects depending on site conditions, burn severity, and nutrient status of the site.

Key words: Ponderosa pine, cone production, seed production, restoration activities, stand thinning.

Historical reconstruction of ponderosa pine, *Pinus ponderosa* Dougl. ex P.&C. Lawson, forests over the last 100 years has shown range-wide significant increases in densities and a concomitant reduction in fire frequency (Covington and Moore 1994, Mast et al. 1997, 1999, Brown and Sieg 1999, Moore et al. 1999, Everett et al. 2000, Veblen et al. 2000, Turner and Krannitz 2001). This has resulted in an emphasis toward restoration of *Pinus ponderosa* forests to reduce tree densities to earlier levels to prevent wildfires, to rejuvenate stands, and to benefit associated wildlife (Covington et al. 1994, Harrod et al. 1999, Mast et al. 1999, Kolb et al. 2001). One wildlife species of interest in the northernmost part of the *P. ponderosa* range is the uncommon and in some places endangered White-headed Woodpecker, *Picoides albolarvatus*. The White-headed woodpecker is most abundant in California, where it relies on seeds from a variety of tree species (Garrett et al. 1996). *Picoides albolarvatus* is a species of concern in Oregon, Washington, and Idaho, while in British Columbia it is nationally endangered. Here, *P. ponderosa* cones provide the only suitable food source in the nonbreeding months (Garrett et al. 1996). In Oregon it is clear that old-growth *Pinus ponderosa* stands, with many snags and large-diameter trees, are more productive for

Picoides albolarvatus than newer and managed stands (Dixon 1995). Restoration activities in Washington state have focused on reintroducing fire to *Pinus ponderosa* ecosystems which, in Methow Valley Ranger District, has resulted in anecdotal reports of increased abundance of *Picoides albolarvatus* (Dale Swedberg personal communication). *Picoides albolarvatus* is the umbrella species of restoration activities in the northern part of the range for *Pinus ponderosa*, and yet there are very little data on the effect of tree thinning and prescribed burning on the ecosystem or the bird. In the Southwest, *Picoides albolarvatus* does not occur, but general effects of tree ingrowth on diversity of native flora and fauna are of concern (Covington and Moore 1994). Here, a research team at Northern Arizona University at Flagstaff has promoted and initiated restoration of *Pinus ponderosa* (Covington et al. 1997) and has begun documenting some of the effects on the ecosystem (i.e., Crawford et al. 2001).

Because of the lack of direct evidence on the benefits of current restoration activities for seed-eating species of interest such as *Picoides albolarvatus*, this review gathers what is known about cone production in *P. ponderosa* in general and assesses whether restoration activities are likely to benefit *Picoides albolarvatus* through enhanced cone production.

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STUDY SPECIES

Taxonomy and Range

Three varieties of *Pinus ponderosa* Dougl. ex P.&C. Lawson are recognized though the taxonomy is not yet resolved: *P. ponderosa* var. *ponderosa* Dougl. (Pacific ponderosa pine), *P. ponderosa* var. *scopulorum* Engelm. (Rocky Mountain ponderosa pine), and *P. ponderosa* var. *arizonica* (Engelm.) Shaw (Arizona pine; Kral 2000). The distribution of *P. ponderosa* ranges from near 52°N in south central and southeastern British Columbia (both *ponderosa* and *scopulorum* subspecies) east to Nebraska, south to northern Mexico (the *arizonica* subspecies), and west to the Pacific Coast (Kral 2000). Within the Pacific variety 3 races (Southern California, Pacific, and North Plateau) have been differentiated (Conkle and Critchfield 1988). There are also 3 races within *P. ponderosa* var. *scopulorum*: Southern, Central, and Northern Interior (Wells 1964).

The *P. ponderosa* environment is broadly characterized by cool to cold winters and warm, dry summers with periods of prolonged drought. Because *P. ponderosa* is the widest ranging pine in North America, the droughts that occur during different seasons in its areas of distribution depend on location. In the Pacific Northwest and California, summers are typically dry, while summer rains are usual for the eastern slope of the Rockies, the Black Hills of South Dakota, and the Southwest (Curtis and Lynch 1957, Hope et al. 1991, Agee 1998). Annual precipitation in the ponderosa pine zone of British Columbia is 280–500 mm (Hope et al. 1991).

The range of *P. ponderosa* encompasses elevations from near sea level at Tacoma, Washington, to between 250 m and 1200 m in British Columbia (Eremko et al. 1989), and to more than 2740 m in California, Colorado, and Arizona (Curtis and Lynch 1957).

Reproductive Cycle
and Seed Production

For 12- to 16-year-old *P. ponderosa* trees in the northern part of the range, seed cones are initiated in mid- to late summer and differentiate in September to October (Eis et al. 1983, Owens and Blake 1985). Pollination occurs between April and June the following year, and pollen tube and ovule development begins and proceeds until midsummer. Development

resumes the next spring, fertilization takes place, and seeds mature by fall. This lengthy (26- to 27-month) reproductive cycle of initiation, differentiation, pollination, fertilization, and embryo and seed development provides a large window for a complex variety of potentially interacting factors to play a role in the frequency of *P. ponderosa* cone production and the quantity of seeds produced (Roeser 1941, Puritch and Vyse 1972, Eis et al. 1983, Owens and Blake 1985, Eremko et al. 1989).

Variability in Productivity

Seed cone production in *Pinus ponderosa* is variable, with 3 broad categories of contributing factors: differences between (1) years, (2) sites, and (3) individual trees (Table 1). Many years result in no cone production at all, and other years result in heavy production, with many cones on more than half the population (McDonald 1992). Throughout its range, these abundant crops occur about every 3 to 8 years (Roeser 1941, Fowells and Schubert 1956, Larson and Schubert 1970, Boldt and van Deusen 1974, Dahms and Barrett 1975, Eis et al. 1983).

Differences in cone production between sites within an area are not as variable, with some site differences being marginally significant (Table 1; data from Dale and Schenk 1978) and others not being significant at all (Table 1; data from Linhart 1988). Within sites, differences in cone production between trees can be striking, with some trees consistently being big producers (Linhart and Mitton 1985).

REGULATION OF SEED
AND CONE PRODUCTION

The 27-month development of a seed-bearing cone provides many opportunities for maternal regulation of seed and cone production via cone, ovule, or embryo abortion. Though *P. ponderosa* cone crops can be decimated by a combination of physiological dysfunction and insect damage, unexplained conelet abortions can prevent as much as 66% of the ovules from becoming seed (Pasek and Dix 1988). Good years for producing cones are also good years for producing seed: over a 24-year period, more filled seeds than unfilled seeds were produced in years with heavy cone production (McDonald 1992).

There has been one study on factors associated with ovule abortion, though it was done

TABLE 1. Variability in seed or cone production for *Pinus ponderosa* (PP). K = 1000.

Location	Variation in seed or cone production	Time period	Comments	Source
California	0–18K seeds · ha ⁻¹ to 400K 1200K seeds · ha ⁻¹ (yearly)	24 years 1958–1981	$r^2 = 0.76$, $P < 0.01$ filled seeds and cone crop, 613 trees · ha ⁻¹	McDonald 1992
Washington	0–384 cones · tree ⁻¹ , 48% variation attributed to year ($P < 0.0001$) and 9% to tree ($P > 0.2$) ^a	7 years 1951–1957	8 different PP trees followed	Daubenmire 1960
Idaho and eastern Washington	0–9.4K cones · 100 PP trees ⁻¹ , 32% variation attributed to site ($P = 0.07$), 28% to year ($P = 0.002$) ^a	3 years 1967–1969	12 widely dispersed sites, 42–770 PP · ha ⁻¹	Dale and Schenk 1978
Colorado	4–12.3K cones · 100 PP trees ⁻¹ , 1.3% variation attributed to site ($P > 0.2$), 42% to year ($P = 0.10$) ^a	4 years 1984–1987	4 sites	Linhart 1987
Arizona	1.2–29.7 cones · 100 PP trees ⁻¹	10 years 1956–1965	62.5 PP · ha ⁻¹	Larson and Shubert 1970
Colorado	0–7.7K cones · 100 PP trees ⁻¹	10 years 1926–1935	78 PP · ha ⁻¹	Roeser 1941
California	0–338 cones · 100 PP trees ⁻¹	21 years 1933–1953	5 PP · ha ⁻¹ , 9 <i>P.</i> <i>lambertiana</i> · ha ⁻¹ , 48 <i>Abies concolor</i> · ha ⁻¹	Fowells and Shubert 1956

^aANOVA, SAS 1990

on a congener of *Pinus ponderosa* (Karkkainen et al. 1999). Seventy-six percent of experimentally self-pollinated ovules in *P. sylvestris* aborted, compared with 26.5% for cross-pollinated and 30% for naturally pollinated ovules. For naturally pollinated seeds, maternal genetic differences accounted for 29% of the variation in ovule abortions (Karkkainen et al. 1999). Unfortunately, no measurements of the effect of environmental variables were made. Ovule abortions have been thought to be associated with self-pollination, temperature, competition, and disease or insect infestation (Owens and Blake 1985, Karlsson 2000).

FACTORS AFFECTING FREQUENCY AND QUANTITY OF CONE CROPS

Factors Contributing to Annual Variation

TEMPERATURE.—Higher-than-average temperatures during seed cone initiation in *P. ponderosa* have been associated with above-average cone production. Over a 23-year period in California, whenever total average temperatures for April and May were above or below average, the cone crop 27 months later was also above or below average, respectively (Maguire 1956). Similarly, in Whitman County,

Washington, larger cone crops of 8 trees over 7 years were correlated with higher-than-average June through September temperatures 2 years earlier (Daubenmire 1960). Temperature effects have also been demonstrated in other *Pinus* species: differences between 1995 and 1996 in cone production in *P. sylvestris* were associated with differences in temperatures at time of bud initiation in 1993 and 1994 (Karlsson 2000).

There is scattered evidence that cold temperatures negatively affect seed cone crops in *P. ponderosa* (Maguire 1956, Schubert 1974, Barrett 1979, Owens and Blake 1985), with below-freezing, late spring temperatures killing 2nd-year conelets (Maguire 1956, Sorensen and Miles 1974). Pollen cones of *P. ponderosa* are less susceptible to freezing (Roeser 1941), as are cones of other pine species such as *P. contorta* (Sorensen and Miles 1974). Negative effects of cold temperatures underscore how weather at any time during the 27-month *P. ponderosa* reproductive cycle might negate or enhance weather effects at another time (Daubenmire 1960).

MOISTURE.—Little information exists on the effects of moisture specific to seed cone production in *P. ponderosa*, and results from other species are conflicting and often confounded

by other factors (Owens and Blake 1985). For example, there is a positive correlation between low rainfall in the spring and summer months when cones are initiated and subsequent cone production, but low moisture is often accompanied by high temperatures and high insolation (Owens and Blake 1985). Anecdotal evidence suggests that reproductive bud initiation in *P. ponderosa* benefits from dry summers (Eis et al. 1983, Eremko et al. 1989). Irrigation in the spring combined with removal of moisture in the summer produced larger cone crops in *P. taeda* than in controls (Dewers and Moehring 1970).

Site-related Factors

STAND DENSITY.—In general, there is an increase in productivity, including seed cone production, with a decrease in stand density. In a comparison of 12 sites in Idaho, seed production was negatively associated with density of both *P. ponderosa* ($r_s = -0.80$, $P = 0.0034$) and all trees ($r_s = -0.67$, $P = 0.017$; data from Dale and Schenk 1978; Spearman rank correlation [SAS 1990]). Similarly, 4 blocks of varying *P. ponderosa* stem densities in Arizona showed concomitant variation in cone and seed production ($r_s = -1.0$, $P < 0.0001$; data from Heidmann 1983). Cone yield differences in response to stand density have been observed for many decades, with individual *P. ponderosa* trees yielding on average 24.7 L of cones in “dense” stands, 38.8 in “medium,” and 63.4 in “open” stands (Pearson 1912).

When *P. ponderosa* stands are thinned, stem diameter of released trees consistently increases (Schubert 1974, Martin 1988, Feeney et al. 1998); this also holds true for older individuals 150+ years of age (Latham and Tappeiner 2002). The responses of stem diameter to reductions in stem density are consistent, and in *Pinus resinosa* they have been predictably modeled (Laroque 2002). Stem diameter is consistently associated with cone production (see section below on tree size, age, and dominance), and the growth response to thinning can be large: *P. ponderosa* stands in the Southwest thinned from 48.21 m² to 6.89 m² basal area · ha⁻¹ grew 5 times faster in diameter than those in unthinned stands (Schubert 1974). Since trees of larger diameter produce the majority of cones, increased cone production may be a longer-term benefit of thinning.

When *P. ponderosa* stands are thinned, photosynthetically active radiation increases (Riegel et al. 1992), and subsequent increases in seed production are often attributed to increased light (Sprague et al. 1979). Evidence from *Pinus* species other than *ponderosa* suggests that an increase in light results in an increase in cone production, either for whole trees (*P. sylvestris*; Sarvas 1962) or individual branches (*P. banksiana*; Despland and Houle 1997). Anecdotal evidence suggests that *P. ponderosa* is similarly dependent on light (Pearson 1912). In addition, changes in the crown location of cone production upon stand thinning showed a localized dependence on light; *P. sylvestris* trees in a closed stand produced 40% of cones in the upper 2 m of crown, and 7 years post-thinning that figure dropped to 15%, with a greater proportion of cones being produced on lower branches that were now exposed to light (Karlsson 2000). These kinds of localized changes in cone production attributable to light are better indicators of the importance of light than whole-tree responses because stand thinning will also affect midday temperatures (Riegel et al. 1992).

NUTRIENT AVAILABILITY AND FERTILIZERS.—Effects of increased nutrients, either added or as a result of thinning, are not as clear as the effect of increased light. Often there is improved flowering and seed production in *Pinus* when fertilization is combined with thinning, irrigation, or girdling treatments (Puritch and Vyse 1972, Owens and Blake 1985). For example, *P. taeda* clones increased seed cone production much more in a combined irrigation and fertilization treatment than in either treatment alone (Sprague et al. 1979, Gregory et al. 1982).

When N alone was added to thinned stands of *P. sylvestris*, an increase in stemwood production occurred, but cone production was lower than that of the controls (Valinger 1993). Adding P along with N at 3 levels of concentration to a thinned, even-aged, 55-year-old *P. ponderosa* stand near Flagstaff, Arizona, resulted in a linear increase of seed cone production (Heidmann 1984). The number of trees bearing cones was always highest in the high fertilizer treatments, and significantly higher in year 4 ($P < 0.025$) and marginally higher in year 5 ($P < 0.1$) of a 6-year study. The period of the experiment encompassed 3 reasonably good

cone crops, with production in these years linearly related to fertilizer levels ($P < 0.05$). During this time period 4 times more cones were produced on trees fertilized at the high rate than in the unfertilized controls (Heidmann 1984).

FIRE EFFECTS.—*Pinus ponderosa* evolved with relatively frequent, but low-intensity, fires (Agee 1988, Arno 1988), and fire suppression over the last 100 years has resulted in dramatic increases in stem density (Harrod et al. 1999, Mast et al. 1999, Turner and Krannitz 2001). From the literature already reviewed, it is clear that thinning results in greater cone production, but there is little direct data on whether or not fire improves production over and above that of thinning. The effect of fire on *P. ponderosa* ecosystems is complex and may be beneficial or detrimental, depending on the nutrient status of the site, initial conditions of the stand, and timing and severity of the burn.

The effect of fire on cone and seed production can be indirectly assessed by its effect on growth because larger trees generally produce more cones (see next section). In unthinned *P. ponderosa* stands, fire was detrimental to growth of surviving trees (Sutherland et al. 1991, Swezy and Agee 1991) largely because of high burn severity attributable to accumulated fuels due to fire suppression. When fire occurred in a thinned stand in Arizona, with the woody debris having been removed prior to the fire, fire improved resin production compared with the thinned treatment and the control (Feeney et al. 1998). This has been associated with increased resistance to insect pests such as the bark beetle (Feeney et al. 1998), which may in turn affect growth and or cone production.

The effect of fire on nutrient availability for *Pinus ponderosa* will be noticeable in cone production (see previous section on nutrient availability). Fire did not affect the rate of N cycling over and above that of thinning in both Arizona (Kaye and Hart 1998) and a nutrient-poor site in Oregon (Monleon et al. 1997), but it decreased total N and organic-matter content (Covington and Sackett 1984, Kaye and Hart 1998). This, however, did not reduce availability of N to the trees because, as also shown by other studies, more of the total N was transformed and made more readily available for uptake (Schoch and Binkley 1986, Knoepp and Swank 1995, Kaye and Hart 1998). Nutrient-

poor *P. ponderosa* sites do not have extra total N to transform, however, and even light surface fires can be detrimental to trees over time in this case (Monleon et al. 1997).

Tree Differences

TREE SIZE, AGE, AND DOMINANCE.—For *Pinus* in general and *Pinus ponderosa* in particular, the largest seed and cone crops are borne by the largest-diameter trees (Fowells and Schubert 1956, Larson and Schubert 1970, Sundahl 1971, Linhart and Mitton 1985, Latta and Linhart 1997, Karlsson 2000). In a 6-year study following more than 200 Colorado *P. ponderosa* trees, diameter was a better predictor of cone production ($r^2 = 0.43$, $P < 0.001$) than age ($P > 0.05$), although diameter and age were correlated ($P < 0.001$; Linhart and Mitton 1985, Latta and Linhart 1997). In California, *P. ponderosa* trees over 66 cm dbh produced at least some cones over a 16-year period, while only 13% of the smallest class (between 9.1 and 19.1 cm dbh) bore cones (Fowells and Schubert 1956). Only *P. ponderosa* trees ≥ 49.5 cm in diameter produced 500 cones or more at least once in the 16-year period (Fowells and Schubert 1956).

Larger-diameter trees also produce cones more frequently. Over a 16-year period in California, frequency of cone production ranged from once for the 19.3–29.2 cm dbh class up to 10 times for all trees larger than 61 cm ($r_s = 0.65$, $P = 0.02$, $n = 12$, for number of crops in 16 years and diameter; data from Fowells and Schubert 1956; Fig. 1). Similarly, in Arizona the frequency of cone crops was highly correlated with tree diameter (Larson and Schubert 1970; Fig. 1). Cone production of 100 cones or more per tree was not as frequent as crops with more than 5 cones, but both classes increased in frequency with diameter (Larson and Schubert 1970; Fig. 1). Frequency of cone production increased linearly with diameter up to approximately 80 cm in diameter, after which it plateaued (Fig. 1). Similarly, cone production in *P. ponderosa* increased with age but the rate of increase was smaller among older trees (Latta and Linhart 1997).

Smaller-diameter *Pinus edulis* produce male cones and larger-diameter trees produce female cones (Floyd 1983). Normally, *Pinus* is considered to be monoecious with both male and female stroboli on the same tree, but size segregation of the sexes has led to the suggestion

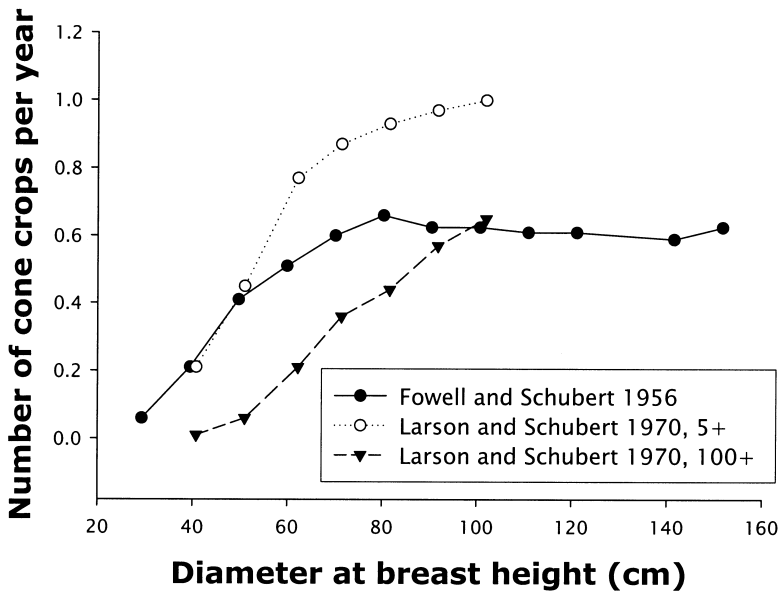


Fig. 1. Relationship between frequency of seed cone crop production and stem diameter of *P. ponderosa*. Data taken from citations listed; 5+ or 100+ refers to cone crops >5 or >100 cones, respectively.

that *Pinus edulis* is functionally dioecious (Floyd 1983). In *P. ponderosa* sex segregation does not occur to this extent, and older trees that produce female cones also produce some male strobili. Younger trees do tend to produce mostly male strobili, with the greatest production occurring from large-diameter young trees (Linhart and Mitton 1985).

Dominant trees, those with crowns extending above the general crown level in a stand, also tend to be more productive than trees whose crowns are in the canopy (co-dominants) or lower (Fowells and Schubert 1956, Larson and Schubert 1970). Tree height alone had a much smaller effect on seed production than did stem diameter; small-diameter but dominant *P. ponderosa* trees in California did not produce seed cones with the same frequency or in the same number as trees of greater diameter (Fowells and Schubert 1956). However, almost all counted cones were borne on dominants (99%), with only 0.92% of total cones produced on co-dominant trees. Intermediate or suppressed crown classes produced only 0.05% of total cones (Fowells and Schubert 1956). Closer inspection of these data shows that the effect of dominance on seed production relates to greater leaf production: seed production in both gymnosperms (including

Pinus ponderosa) and angiosperms is directly associated with leaf mass (Greene and Johnson 1994).

COMPETITION.—The largest *P. ponderosa* cone crops are produced by isolated trees that are free from competition. Over 10 years in central Arizona, isolated trees free to grow on all sides not only produced cone crops more frequently but also averaged 274 cones per year versus 158 cones for open stands, 90 cones for trees on the margin of stands, and 42 cones for interior trees (Larson and Schubert 1970). Some benefits of reductions in stand density mentioned earlier can be attributed to reduced competition for resources such as light. The only caveat is while low stand densities are beneficial for cone production, isolated *P. ponderosa* trees self-pollinate at a higher frequency than stand-grown trees, and self-pollinated cones bear lower percentages of filled seed (Sorensen and Miles 1974). *Pinus ponderosa* seedlings from seeds of lower-density stands are also more inbred and have lower heterozygosity and survival ability (Farris and Mitton 1984).

Competition with the understory shrub layer for resources other than light also plays a role in *P. ponderosa* growth (Oliver 1984, McDonald and Abbott 1997). In a northern California

plantation, *P. ponderosa* grew to 20 cm in diameter in 31 years without competition from shrubs, whereas with a heavy shrub cover diameters averaged 5.4 cm (McDonald and Abbott 1997). Similarly in Oregon, *P. ponderosa* trees 13 cm to 51 cm in diameter (19 to 36 years old) added an average of 7.6 cm in diameter over 10 years when surrounded by understory vegetation, but they averaged 16.5 cm without surrounding ground cover (Dahms and Silen 1956, cited in Barrett 1979). Reduced growth was associated with greater susceptibility to damage by insects (Oliver 1984, McDonald and Abbott 1997).

GENETICS.—Genetic differences were suspected a number of years ago when Linhart et al. (1979) observed that only a few *Pinus* trees produced the majority of cones. *Pinus ponderosa* trees that produce abundant cone crops were shown to be genetically distinct from those that did not (Linhart et al. 1979). *Pinus ponderosa* and *P. sylvestris* trees of the same diameter produce either abundant cone crops or many male strobili, but not both in abundance (*P. ponderosa*: Linhart and Mitton 1985; *P. sylvestris*: Savolainen et al. 1993). Trees that produce both produce fewer of each (Linhart and Mitton 1985, Savolainen et al. 1993). In addition, individual trees that are genetically predisposed for high female cone production bear a cost in vegetative growth: they have smaller stem diameters than *P. ponderosa* trees with low cone production of the same age (Linhart et al. 1979).

Recently, plantations of genetic clones of a variety of *Pinus* species showed that seed cone production has a strong genetic component (*P. banksiana*: Todhunter and Polk 1981; *P. nigra*: Matziris 1993; *P. sylvestris*: Burczyk and Chalupka 1997). For *P. sylvestris*, variation in cone production attributable to different clones exceeded that for differences between years, but in both cases data were collected for only 2 years (Savolainen et al. 1993, Burczyk and Chalupka 1997). Byram et al. (1986), monitoring clonal plantations over many years, noted that clones of *P. taeda* would change rank from year to year in cone production.

SILVICULTURAL INDUCEMENTS FOR CONE PRODUCTION

A variety of silvicultural treatments have been used in *Pinus* seed orchards to increase

seed and cone production (see review within Eriksson et al. 1998). In *P. ponderosa* only girdling has been applied, with varying success. Wide (2.5 cm to 5 cm, with small bridge) and narrow girdling (cut around entire circumference) were applied during bud initiation in May in western Montana, and both methods increased cone production of the 1st crop to be formed post-treatment, although some treated trees showed no response (Shearer and Schmidt 1970). On average, treated trees produced about 20 cones versus 1 cone produced by the paired controls (Shearer and Schmidt 1970). The treatment had no lasting effect in subsequent years.

FACTORS AFFECTING SEED AND CONE LOSS

Insects

The native pines of North America host at least 1111 insect species, and *Pinus ponderosa* hosts 367 of them, the highest for any pine (de Groot and Turgeon 1998). Nine species are associated with pollen cones and 35 species are associated with seed cones (de Groot and Turgeon 1998). Other insects, not specialized on cones, may also affect production by weakening or killing trees outright (e.g., pine beetles, *Dendroctonus* spp.; Curtis and Lynch 1957, Oliver and Ryker 1990, de Groot and Turgeon 1998).

While pollen cone insects may be relatively benign (Hedlin et al. 1980), seed cone insects can destroy high proportions of cone crops in some years (Larson and Schubert 1970, de Groot and Turgeon 1998). The coneworm, *Dioryctria auranticella* (Grote), for example, killed 80% of *P. ponderosa* cones in interior British Columbia (Ross and Evans 1957) and northern Arizona (Blake et al. 1989), and up to 57% in Idaho (Dale and Schenk 1978). At 10 sites in northern Arizona, seed damage by all insect pests, including the coneworm, ranged from a low of 1% to a high of 91% per cone (Schmid et al. 1984). Survival of 1st season conelets can be especially difficult: survival averaged only 19.5%, and 76.8% of those survived a 2nd year (Pasek and Dix 1988).

Diseases

As with insects, diseases of *Pinus ponderosa* are many and may reduce cone production directly or indirectly by undermining tree

health. Dwarf mistletoe, *Arceuthobium* spp., is *P. ponderosa*'s most widespread disease and causes the most damage (Oliver and Ryker 1990). In the Southwest it has been particularly devastating and is sometimes responsible for significant mortality (Schubert 1974). Among trees that survive, the parasite impairs tree growth and reduces seed production and seed viability (Schubert 1974, Hawksworth and Shaw 1988, Harrington and Wingfield 1998). *Elytroderma deformans* is *P. ponderosa*'s most serious foliage disease and may slow the growth of mature trees, occasionally killing them. Bark beetles may also be quick to attack affected trees, which, like trees parasitized by *Arceuthobium*, develop characteristic witches' brooms (Curtis and Lynch 1957, Oliver and Ryker 1990, Harrington and Wingfield 1998).

Other pathogens that significantly affect *P. ponderosa* include species of *Armillaria* and a diverse assemblage of parasites, cankers, root diseases, heart rots, foliage diseases, blights, and rusts (Oliver and Ryker 1990), many of which have benefited from fire suppression as well as from leftover stumps from thinning and harvest operations (Harrington and Wingfield 1998). Diseases might be more prevalent at higher stand densities; in *P. sylvestris* higher stand densities increased susceptibility to a canker (Niemela et al. 1992).

Other Animals

Squirrels (*Tamiasciurus hudsonicus*, *Sciurus aberti*, and *S. kaibabensis*) destroy potential cone crops by vigorously clipping conelet-bearing twigs and directly clipping cones and consuming seeds (Keith 1965, Larson and Schubert 1970, Snyder 1993). In the southern part of the *P. ponderosa* range, *Sciurus aberti* reduced cone production of target trees to 10% that of nontarget trees (Snyder 1993). White-headed Woodpeckers and other woodpeckers are also *P. ponderosa* seed predators (Garrett et al. 1996), but their effect on overall seed and cone production has not been quantified.

CONCLUSION

Restoration activities in natural stands of *P. ponderosa* include thinning and fire, in combination and alone. Research on *P. ponderosa* and other *Pinus* species suggests that thinning increases cone production through greater light availability, reduced competition for nutri-

ents and water, increased temperature, and reduced disease and insect pests. These in turn have been shown to promote growth in stem diameter, which is strongly linked to cone production. The only negative issue with respect to thinning is the possibility of self-pollination that leads to greater ovule abortion. The effect of fire is less clear, but limited evidence suggests that combining fire with thinning is the best way to improve health, growth, and cone production in *P. ponderosa* stands.

Factors that influence cone production, but that are not normally controlled in natural *P. ponderosa* stands, include climate, which may affect annual variation and crop failures; genetics, with only some trees being genetically predisposed to produce large cone crops; and seed predators, which in some areas can be responsible for substantial seed loss.

What does this all mean for the White-headed Woodpecker? Thinning treatments being carried out in the northern part of the *P. ponderosa* range will certainly increase seed and cone production unless the trees that are removed are the ones that are genetically predisposed for greater seed and cone production. However, given the benefits of outcrossing, a few younger trees that predominantly produce pollen should also be left in the stand.

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LITERATURE CITED

- AGEE, J.K. 1998. Fire and pine ecosystems. Pages 193–218 in D.M. Richardson, editor, *Ecology and biogeography of Pinus*. Cambridge University Press, New York.
- ARNO, S.F. 1988. Fire ecology and its management implications in ponderosa pine forests. Pages 133–139 in D.M. Baumgartner and J.E. Lotan, editors, *Ponderosa pine: the species and its management*. Symposium proceedings, Spokane, WA, 29 September–1 October 1987. Washington State University Publications, Pullman.
- BARRETT, J.W. 1979. *Silviculture of ponderosa pine in the Pacific Northwest: the state of our knowledge*. U.S. Department of Agriculture, Forest Service General Technical Report PNW-97, Portland, OR.
- BLAKE, E.A., M.R. WAGNER, AND T.W. KOERBER. 1989. Relative effect of seed and cone insects on ponderosa pine in northern Arizona. *Journal of Economic Entomology* 82:1691–1694.

- BOLDT, C.E., AND J.L. VAN DEUSEN. 1974. Silviculture of ponderosa pine in the Black Hills: the status of our knowledge. U.S. Department of Agriculture, Forest Service Report RM-124, Fort Collins, CO.
- BROWN, P.M., AND C.H. SIEG. 1999. Historical variability in fire at the ponderosa pine—Northern Great Plains prairie ecotone, southeastern Black Hills, South Dakota. *Ecoscience* 6:539–547.
- BURCZYK, J., AND W. CHALUPKA. 1997. Flowering and cone production variability and its effect on parental balance in a Scots pine clonal seed orchard. *Annales des Sciences Forestieres (Paris)* 54:129–144.
- BYRAM, T.D., W.J. LOWE, AND J.A. MCGRIFF. 1986. Clonal and annual variation in cone production in loblolly pine seed orchards. *Forestry* 32:1067–1073.
- CONKLE, M.T., AND W.B. CRITCHFIELD. 1988. Genetic variation and hybridization of ponderosa pine. Pages 27–43 in D.M. Baumgartner and J.E. Lotan, editors, *Ponderosa pine: the species and its management*. Symposium proceedings, Spokane, WA, 29 September–1 October 1987. Washington State University Publications, Pullman.
- COVINGTON, W.W., AND M.M. MOORE. 1994. Post settlement changes in natural fire regimes and forest structure: ecological restoration of old-growth ponderosa pine forests. *Journal of Sustainable Forestry* 2:153–181.
- COVINGTON, W.W., AND S.S. SACKETT. 1984. The effect of a prescribed burn in southwestern ponderosa pine on organic matter and nutrients in woody debris and forest floor. *Forest Science* 30:183–192.
- COVINGTON, W.W., R.L. EVERETT, R. STEELE, L.L. IRWIN, T.A. DERR, AND A.N.D. AUCLAIR. 1994. Historical and anticipated changes in forest ecosystems of the inland west of the United States. *Journal of Sustainable Forestry* 2:13–63.
- COVINGTON, W.W., P.Z. FULÉ, M.M. MOORE, S.C. HART, T.E. KOLB, J.N. MAST, S. SACKETT, AND M.R. WAGNER. 1997. Restoring ecosystem health in ponderosa pine forests of the Southwest. *Journal of Forestry* 95: 23–29.
- CRAWFORD, J.A., C.-H.A. WAHREN, S. KYLE, AND W.H. MOIR. 2001. Responses of exotic plant species to fires in *Pinus ponderosa* forests in northern Arizona. *Journal of Vegetation Science* 12:261–268.
- CURTIS, J.D., AND D.W. LYNCH. 1957. Silvics of ponderosa pine. U.S. Department of Agriculture, Forest Service Miscellaneous Publication 12, Intermountain Forest and Range Experiment Station, Ogden, UT.
- DAHMS, W.G., AND J.W. BARRETT. 1975. Seed production of central Oregon ponderosa and lodgepole pines. U.S. Department of Agriculture, Forest Service Report PNW-191, Portland, OR.
- DALE, J.W., AND J.A. SCHENK. 1978. Cone production and insect-caused seed losses of ponderosa pine in Idaho and adjacent Washington and Montana. *Bulletin* 24, University of Idaho, Forest, Wildlife and Range Experiment Station, Moscow.
- DAUBENMIRE, R.F. 1960. A seven-year study of cone production as related to xylem layers and temperature in *Pinus ponderosa*. *American Midland Naturalist* 64:189–193.
- DE GROOT, P., AND J.J. TURGEON. 1998. Insect-pine interactions. Pages 354–380 in D.M. Richardson, editor, *Ecology and biogeography of Pinus*. Cambridge University Press, New York.
- DESPLAND, E., AND G. HOULE. 1997. Aspect influences cone abundance within the crown of *Pinus banksiana* Lamb. trees at the limit of the species distribution in northern Quebec (Canada). *Ecoscience* 4: 521–525.
- DEWERS, R.S., AND D.M. MOEHRING. 1970. Effect of soil water stress on initiation of ovulate primordia in loblolly pine. *Forest Science* 16:219–221.
- DIXON, R.D. 1995. Ecology of White-headed Woodpeckers in the central Oregon Cascades. Master's thesis, University of Idaho, Moscow.
- EIS, S., D. CRAIGDALLIE, AND G.R. POWELL. 1983. Reproduction of conifers: a handbook for cone crop assessment. Technical Report 31, Canadian Forestry Service, Ottawa, Ontario.
- EREMKO, R.D., D.G.W. EDWARDS, AND D. WALLINGER. 1989. A guide to collecting cones of British Columbia conifers. Forest Resource Development Agency Report 055, Forestry Canada and British Columbia Ministry of Forests, Victoria, British Columbia.
- ERIKSSON, U., G. JANSSON, AND C. ALMQVIST. 1998. Seed and pollen production after stem injections of gibberellin A₄₇ in field-grown seed orchards of *Pinus sylvestris*. *Canadian Journal of Forest Research* 28: 340–346.
- EVERETT, R.L., R. SCHELLHASS, D. KEENUM, D. SPURBECK, AND P. OHLSON. 2000. Fire history in the ponderosa pine/Douglas-fir forest on the east slope of the Washington Cascades. *Forest Ecology and Management* 129:207–225.
- FARRIS, M.A., AND J.B. MITTON. 1984. Population density, outcrossing rate and heterozygote superiority in ponderosa pine. *Evolution* 38:1151–1154.
- FEENEY, S.R., T.E. KOLB, W.W. COVINGTON, AND M.R. WAGNER. 1998. Influence of thinning and burning restoration treatments on presettlement ponderosa pines at the Gus Pearson Natural Area. *Canadian Journal of Forest Research* 28:1295–1306.
- FLOYD, M.E. 1983. Dioecy in five *Pinus edulis* populations in the southwestern United States. *American Midland Naturalist* 110:405–411.
- FOWELLS, H.A., AND G.H. SCHUBERT. 1956. Seed crops of forest trees in the pine region of California. U.S. Department of Agriculture, Technical Bulletin 1150, Government Print Office, Washington, DC.
- GARRETT, L.K., M.G. RAPHAEL, AND R.D. DIXON. 1996. White-headed Woodpecker (*Picoides albolarvatus*). No. 252 in A. Poole and F. Gill, editors, *The birds of North America*. The Academy of Natural Sciences, Philadelphia, PA, and the American Ornithologists' Union, Washington, DC. 23 pp.
- GREENE, D.F., AND E.A. JOHNSON. 1994. Estimating the mean annual seed production of trees. *Ecology* 75: 642–647.
- GREGORY, J.D., W.M. GUINNESS, AND C.B. DAVEY. 1982. Fertilization and irrigation stimulate flowering and cone production in a loblolly pine *Pinus taeda* seed orchard. *Southern Journal of Applied Forestry* 6: 44–48.
- HARRINGTON, T.C., AND M.J. WINGFIELD. 1998. Diseases and the ecology of indigenous and exotic pines. Pages 381–404 in D.M. Richardson, editor, *Ecology and biogeography of Pinus*. Cambridge University Press, New York.
- HARROD, R.J., B.H. MCRAE, AND W.E. HARTL. 1999. Historical stand reconstruction in ponderosa pine forest to guide silvicultural prescriptions. *Forest Ecology and Management* 114:433–446.

- HAWKORTH, F.G., AND C.G. SHAW III. 1988. Damage and control of major diseases of ponderosa pine. Pages 99–108 in D.M. Baumgartner and J.E. Lotan, editors, *Ponderosa pine: the species and its management*. Symposium proceedings, Spokane, WA, 29 September–1 October 1987. Washington State University Publications, Pullman.
- HEDLIN, A.F., H.O. YATES III, D.C. TOYAR, B.H. EBEL, T.W. KOERBER, AND E.P. MERKEL. 1980. Cone and seed insects of North American conifers. Environment Canada, Canadian Forest Service, Ottawa, Canada; USDA Forest Service, Washington, DC; Universidad Autonoma Chapingo, Chapingo, Mexico.
- HEIDMANN, L.J. 1983. Seed production in southwestern ponderosa pine on a sedimentary soil. U.S. Department of Agriculture, Forest Service Research Note RM-434, Fort Collins, CO.
- _____. 1984. Fertilization increases cone production in a 55-year-old ponderosa pine stand in central Arizona. *Forest Science* 30:1079–1083.
- HOPE, G.D., D.A. LLOYD, W.R. MITCHELL, W.R. ERICKSON, W.L. HARPER, AND B.M. WIKEEM. 1991. Ponderosa pine zone. Pages 139–151 in D. Meidinger and J. Pojar, editors, *Ecosystems of British Columbia*. British Columbia, Ministry of Forests, Victoria, British Columbia.
- KARKKAINEN, K., O. SAVOLAINEN, AND V. KOSKI. 1999. Why do plants abort so many developing seeds: bad offspring or bad maternal genotypes? *Evolutionary Ecology* 13:305–317.
- KARLSSON, C. 2000. Seed production of *Pinus sylvestris* after release cutting. *Canadian Journal of Forest Research* 30:982–989.
- KAYE, J.P., AND S.C. HART. 1998. Ecological restoration alters nitrogen transformations in a ponderosa pine–bunchgrass ecosystem. *Ecological Applications* 8: 1052–1060.
- KEITH, J.O. 1965. The Abert squirrel and its dependence on ponderosa pine. *Ecology* 46:150–163.
- KNOEPP, J.D., AND W.T. SWANK. 1995. Comparison of available soil nitrogen assays in control and burned forest sites. *Soil Science Society of America Journal* 59: 1750–1754.
- KOLB, T.E., P.Z. FULE, M.R. WAGNER, AND W.W. COVINGTON. 2001. Six-year changes in mortality and crown condition of old-growth ponderosa pines in ecological restoration treatments at the G.A. Pearson Natural Area. Pages 61–66 in R.K. Vance, C.B. Edminster, W.W. Covington, and J.A. Blake, editors, *Ponderosa pine ecosystems restoration and conservation: steps towards stewardship*. Conference proceedings, Flagstaff, AZ, 25–27 April 2000. U.S. Department of Agriculture, Forest Service Report RMRS-P-22, Rocky Mountain Research Station, Ogden, UT.
- KRAL, R. 2000. *Pinus* Linnaeus in Flora of North America north of Mexico. Volume 2: Pteridophytes and gymnosperms [on-line]. Flora of North America Association. Available from <http://hua.huh.harvard.edu/FNA/> [cited 5 April 2002].
- LAROQUE, G.R. 2002. Examining different concepts for the development of a distance-dependent competition model for red pine diameter growth using long-term stand data differing in initial stand density. *Forest Science* 48:24–34.
- LARSON, M.M., AND G.H. SCHUBERT. 1970. Cone crops of ponderosa pine in central Arizona including the influence of Abert squirrels. U.S. Department of Agriculture, Forest Service Report RM-58, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.
- LATHAM, P., AND J. TAPPEINER. 2002. Response of old-growth conifers to reduction in stand density in western Oregon forests. *Tree Physiology* 22:137–146.
- LATTA, R.G., AND Y.B. LINHART. 1997. Path analysis of natural selection on plant chemistry: the xylem resin of ponderosa pine. *Oecologia* 109:251–258.
- LINHART, Y.B., 1988. Ecological and evolutionary studies of ponderosa pine in the Rocky Mountains. Pages 77–89 in D.M. Baumgartner and J.E. Lotan, editors, *Ponderosa pine: the species and its management*. Symposium proceedings, Spokane, WA, 29 September–1 October 1987. Washington State University Publications, Pullman.
- LINHART, Y.B., AND J.B. MITTON. 1985. Relationships among reproduction, growth rates, and protein heterozygosity in ponderosa pine. *American Journal of Botany* 72:181–184.
- LINHART, Y.B., J.B. MITTON, D.M. BOWMAN, K.B. STURGEON, AND J.L. HAMRICK. 1979. Genetic aspects of fertility differentials in ponderosa pine (*Pinus ponderosa* var. *scopulorum*). *Genetical Research* 33:237–242.
- MAGUIRE, W.P. 1956. Are ponderosa pine crops predictable? *Journal of Forestry* 54:778–779.
- MARTIN, F.C., 1988. Effects of site, age and density on growth of ponderosa pine in western Montana. Pages 261–271 in D.M. Baumgartner and J.E. Lotan, editors, *Ponderosa pine: the species and its management*. Symposium proceedings, Spokane, WA, 29 September–1 October 1987. Washington State University Publications, Pullman.
- MAST, J.N., T.T. VEBLE, AND M.E. HODGSON. 1997. Tree invasion within a pine/grassland ecotone: an approach with historic aerial photography and GIS modeling. *Forest Ecology and Management* 93:181–194.
- MAST, J.N., P.Z. FULE, M.M. MOORE, W.W. COVINGTON, AND A.E.M. WALTZ. 1999. Restoration of presettlement age structure of an Arizona ponderosa pine forest. *Ecological Applications* 9:228–239.
- MATZIRIS, D. 1993. Variation in cone production in a clonal seed orchard of black pine. *Silvae Genetica* 42: 136–141.
- MCDONALD, P.M. 1992. Estimating seed crops of conifer and hardwood species. *Canadian Journal of Forest Research* 22:832–838.
- MCDONALD, P.M., AND C.S. ABBOTT. 1997. Vegetation trends in a 31-year-old ponderosa pine plantation: effect of different shrub densities. U.S. Department of Agriculture, Forest Service Report PSW-RP-231, Pacific Southwest Forest and Range Experiment Station, Albany, CA.
- MONLEON, V.J., K. CROMACK JR., AND J.D. LANDSBERG. 1997. Short- and long-term effects of prescribed underburning on nitrogen availability in ponderosa pine stands in central Oregon. *Canadian Journal of Forest Research* 27:369–378.
- MOORE, M.M., W.W. COVINGTON, AND P.Z. FULE. 1999. Reference conditions and ecological restoration: a southwestern ponderosa pine perspective. *Ecological Applications* 9:1266–1277.
- NIEMELA, P., M. LINDGREN, AND A. UOTILA. 1992. The effect of stand density on the susceptibility of *Pinus sylvestris* to *Gremmeniella-abientina*. *Scandinavian Journal of Forest Research* 7:129–133.

- OLIVER, W.W. 1984. Brush reduced growth of thinned ponderosa pine in northern California. U.S. Department of Agriculture, Forest Service Report PSW-172, Pacific Southwest Forest and Range Experiment Station, Berkeley, CA.
- OLIVER, W.W., AND R.A. RYKER. 1990. *Pinus ponderosa* Dougl. ex Laws. Pages 413–424 in R.M. Burns and B.H. Honkala, editors, *Silvics of North America agriculture handbook 654*. Volume 1: Conifers. U.S. Department of Agriculture, Washington, DC.
- OWENS, J.N., AND M.D. BLAKE. 1985. Forest tree seed production: a review of literature and recommendations for future research. Canadian Forest Service Report P1-X-53, Petawawa National Forest Service, Ottawa, Ontario.
- PASEK, J.E., AND M.E. DIX. 1988. Insect damage to conelets, second-year cones, and seeds of ponderosa pine in southeastern Nebraska. *Journal of Economic Entomology* 81:1681–1690.
- PEARSON, G.H. 1912. The influence of age and condition of the tree upon seed production in western yellow pine. U.S. Forest Service Circular 196, Government Print Office, Washington, DC.
- PURITCH, G.S., AND A.H. VYSE. 1972. Cone production in conifers: a review of the literature and evaluation of research needs. Canadian Forest Service Report BC-X-65, Pacific Forestry Center, Victoria, British Columbia.
- RIEDEL, G.M., R.F. MILLER, AND W.C. KRUEGER. 1992. Competition for resources between understory vegetation and overstory *Pinus ponderosa* in northeastern Oregon. *Ecological Applications* 2:71–85.
- ROESER, J., JR. 1941. Some aspects of flower and cone production of ponderosa pine. *Journal of Forestry* 39: 534–536.
- ROSS, D.A., AND D. EVANS. 1957. Annotated list of forest insects of British Columbia. Part V: *Dioryctria* spp. (Pyralidae). *Proceedings of the Entomological Society of British Columbia* 53:10–11.
- SARVAS, R. 1962. Investigations on the flowering and seed crop of *Pinus sylvestris*. *Communications Instituti Forestalis Fenniae* 53:1–198.
- SAS INSTITUTE, INC. 1990. SAS user's guide. Volume 2, 4th edition. Cary, NC.
- SAVOLAINEN, O., K. KARKKAINEN, A. HARJU, T. NIKKANEN, AND M. RUSANEN. 1993. Fertility variation in *Pinus sylvestris*: a test of sexual allocation theory. *American Journal of Botany* 80:1016–1020.
- SCHMID, J.M., J.C. MITCHELL, K.D. CARLIN, AND M.R. WAGNER. 1984. Insect damage, cone dimensions, and seed production in crown levels of ponderosa pine. *Great Basin Naturalist* 44:575–578.
- SCHOCH, P., AND D. BINKLEY. 1986. Prescribed burning increased nitrogen availability in a mature loblolly pine stand. *Forest Ecology and Management* 14:13–22.
- SCHUBERT, G.H. 1974. Silviculture of southwestern ponderosa pine: the status of our knowledge. U.S. Department of Agriculture, Forest Service Report RM-123, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.
- SHEARER, R.C., AND W.C. SCHMIDT. 1970. Natural regeneration in ponderosa pine forests of western Montana. U.S. Department of Agriculture, Forest Service Report INT-86, Ogden, UT.
- SNYDER, M.A. 1993. Interactions between Abert's squirrel and ponderosa pine: the relationship between selective herbivory and host plant fitness. *American Naturalist* 141:866–879.
- SORENSEN, F.C., AND R.S. MILES. 1974. Self-pollination effects on Douglas-fir and ponderosa pine seeds and seedlings. *Silvae Genetica* 23:135–138.
- SPRAGUE, J., J.B. JETT, AND B. ZOBEL. 1979. The management of southern pine seed orchards to increase seed production. Pages 145–162 in F. Bonner, editor, *Flowering and seed development in trees*. Symposium proceedings, New Orleans, LA, 15–18 May 1978. Mississippi State University, Starkville.
- SUNDAHL, W.E. 1971. Seedfall from young growth ponderosa pine. *Journal of Forestry* 69:790–792.
- SUTHERLAND, E.K., W.W. COVINGTON, AND S. ANDARIESE. 1991. A model of ponderosa pine growth response to prescribed burning. *Forest Ecology and Management* 44:161–173.
- SWEZY, D.M., AND J.K. AGEE. 1991. Prescribed fire effects on fine root and tree mortality in old-growth ponderosa pine. *Canadian Journal of Forest Research* 21:626–634.
- TODHUNTER, M.N., AND R.B. POLK. 1981. Seed and cone production in a clonal orchard of Jack pine (*Pinus banksiana*). *Canadian Journal of Forest Research* 11: 512–516.
- TURNER, J.S., AND P.G. KRANNITZ. 2001. Conifer density increases in semi-desert habitats of British Columbia in the absence of fire. *Northwest Science* 75:176–182.
- VALINGER, E. 1993. Effects of thinning and nitrogen fertilization on growth of Scots pine trees: total annual biomass increment, needle efficiency, and above-ground allocation of biomass increment. *Canadian Journal of Forest Research* 23:1639–1644.
- VEBLEN, T.T., T. KITZBERGER, AND J. DONNEGAN. 2000. Climatic and human influences on fire regimes in ponderosa pine forests in the Colorado Front Range. *Ecological Applications* 10:1178–1195.
- WELLS, O.O. 1964. Geographic variation in ponderosa pine I. The ecotypes and their distribution. *Silvae Genetica* 13:89–103.

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