

# On the relationship between pollen capture and seed set in conifers

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**Abstract:** A log-log function ( $\log Y = \log a + b \log X$ ) is used to model the relationship between seed yield and pollen capture (PC) as estimated with field samplers. In this model,  $Y$  is seed yield,  $X$  is estimated PC, and  $\log a$  and  $b$  are, respectively, intercept and slope of the linear relationship between  $\log X$  and  $\log Y$ . The model indicates that seed set increases rapidly with initial increase in PC, and closely approaches or reaches an asymptote at PC values that are low compared with maximum PCs measured in field situations.

**Résumé :** Les auteurs ont employé une fonction logarithmique double ( $\log Y = \log a + b \log X$ ) afin de modéliser la relation entre la production semencière et la quantité de pollen piégé (PC) estimée à l'aide de trappes d'échantillonnage au champ. Dans ce modèle,  $Y$  représente la production semencière,  $X$  est l'estimation de PC, alors que  $\log a$  et  $b$  représentent respectivement l'ordonnée à l'origine et la pente de la relation linéaire entre  $\log X$  et  $\log Y$ . L'application du modèle indique que la production semencière augmente rapidement avec l'augmentation initiale de PC. Elle atteint progressivement un plateau asymptotique pour des valeurs de PC qui sont faibles comparativement aux valeurs maximales de PC mesurées au champ.

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## Introduction

Most temperate zone conifers are monoecious, wind pollinated, and pollen shed overlaps with seed cone receptivity on the same plant (Silen 1979). Within a stand or population, the bulk of the flowering generally occurs over a few days to a few weeks, with the duration depending on weather conditions at the time of flowering. The same is true for individual seed cones within a tree where receptive time and duration varies with temperature, aspect, and crown height. Conifers also display variation in reproductive behavior between years; there is considerable variation among species but in general abundant seed crops are produced every 7–10 years interspersed with light and moderate crops (Owens and Blake 1985). Stands can vary in size, tree density, and species representation. The consequence of this variability is that density of pollen in the air can vary greatly for different strobili. The purpose of this paper is to consider the effect of pollen capture (PC) on seed set and to propose several simple mathematical models that describe the relationship between the two. A broadly applicable model that could be used to relate seed set to PC could be of value in judging the consequences of pollen management, including quantifying of contaminant pollen, and possibly helpful in interpreting the genetic effects of long-distance pollen flight and of population size, particularly with reference to small populations.

Although a number of factors, such as prevailing wind direction, crown position, and natural selfing might disturb the

relationship (Smith et al. 1988; Di-Giovanni and Kevan 1991), several observations in the literature suggest (1) that seemingly low densities of pollen are quite effective in fertilization and (2) that seed set closely approaches or is maximum at moderate or intermediate values of PC. Where increasing PC is not associated with an increase in seed set, we have termed this PC value as 100% pollen load.

First, we mention some observations on the efficacy of low PC. Squillace (1967) reported nearly normal seed set in a young slash pine (*Pinus elliotii* Engelm.) seed orchard that had been hand emasculated, was surrounded by a 400-ft isolation band, and was bounded by mature longleaf pine (*Pinus palustris* Mill.) in several directions. PC was not measured, but the implication was that a relatively small amount of contaminant pollen resulted in good seed set. In lodgepole pine (*Pinus contorta* Dougl. ex Loud.), percent filled seed was significantly correlated with density of conspecific trees, but even in stands of low density, or in mixed stands with lodgepole as a very minor component, percent filled seed was quite high (Smith et al. 1988; Sorensen and Adams 1993). F.C. Sorensen and D.W. Cress (unpublished data) collected cones in a Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) orchard in two years, one year with a light pollen crop and a second year with a large, induced pollen crop. Filled seed percents for the two years were similar, 55.9% the first year vs. 56.9% the second. Nilsson (1995) reports that "low availability of pollen in the air" was not a limiting factor for fertilization in a *Pinus sylvestris* L. orchard in central Sweden.

Comparable observations come from a young 0.5-ha plantation of noble fir (*Abies procera* Rehd.) growing in the Willamette Valley of Oregon and a young Sitka spruce (*Picea sitchensis* (Bong.) Carrière) seed orchard on the east side of the Olympic Mountains in Washington (F.C. Sorensen and L.E. Smith, unpublished data). The noble fir plantation is about 30 km east of the nearest noble fir stand and about 800 m lower in elevation. Average percent filled seed for cones collected from 32 trees was 48.0%, which was almost the same as that

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reported for an extensive native mature stand in the Oregon Cascade Mountains in a good cone year (46.4%) (Sorensen et al. 1976). The Washington Sitka spruce orchard contained 50 clones with a total of 350 ramets and was many kilometers from other stands of the same species. Sixty-one trees produced pollen in 1993 of which 43 had a few catkins on a few twigs, 14 had a few catkins on many twigs, and 4 had many catkins on many twigs. Cones were collected from 15 ramets well distributed throughout the orchard. Percent filled seed for these trees averaged 33.3%, compared with 60–70% filled seed in a very good cone year in a natural old-growth spruce–hemlock stand (Harris 1969). Pollen densities were not recorded for these two locations, but seed set seemed surprisingly high given the number of pollen-producing trees. Again, the implication to us was that pollen densities that were probably low compared with normal stands gave relatively high seed sets.

Second, other observations indicate that once intermediate seed sets are reached, additional pollen is much less effective in increasing seed yield. For example, Wheeler and Jech (1986a) reported on the effectiveness of supplemental mass pollination (SMP) treatment in a Douglas-fir orchard in which a blower was used to deliver the pollen. The success rate of SMP, defined as the proportion of seed arising from the SMP application, was measured with isozyme analysis. Although SMP treatment resulted in 42% SMP-fertilized seeds in the treated cones, percent filled seed was increased only from 48% to 63%. PC values and SMP efficiencies recorded by Wheeler and Jech (1986a) were on the high end of operational experience (El-Kassaby et al. 1993; Webber 1995), but the Wheeler–Jech observations are evidence that a large change in PC, when PC values are already high, can have a much less than equivalent effect on seed set.

## Materials and methods

### The models

As noted in the Introduction, our inference from these varied observations is that modest PC is quite effective in fertilization and that seed sets approach maximum at moderate values of PC. Initial work by Bramlett (1977) and Bramlett and O'Gwynn (1981), in which seed set was related to applied pollen quantity in controlled-pollination tests, showed that the log–log transformed power function ( $\log Y = \log a + b \log X$ , where  $Y$  is seed set in filled seed or percent filled seed per cone,  $X$  is pollen quantity, and  $\log a$  and  $b$  are the intercept and slope, respectively, of the line after log transformation) gave very high coefficients of determination ( $R^2$ ) of 0.972 and 0.960, respectively, for pollen quantities less than 100% pollen load. Such high  $R^2$  values suggested that the relationship between seed set and PC as monitored in natural stands or in seed orchards might be modelled with the same equation.

Additional models were chosen for testing based on field experience and intuitive reasoning. Since the number of ovules per cone is finite, each incremental increase in PC is not proportional to a similar increase in seed yield. At low PCs, the relationship of PC to seed set may be approximately linear, but at higher PCs it should be increasingly asymptotic. Based on these inferences, we tested four nonlinear models: power ( $Y = aX^b$ ), exponential ( $Y = a e^{bX}$ ), negative exponential [ $Y = a(1 - e^{-bX})$ ], and logistic [ $Y = a/(1 + e^{b-cX})$ ], where  $X$  and  $Y$  are defined as above,  $e$  is the exponential constant ( $e = 2.72$ ), and  $a$ ,  $b$ , and  $c$  are fitted constants. The negative exponential function was suggested by Gregorius (1983), but he did not have data with which

to test it. The fit of our data sets to the models is compared based on adjusted coefficients of determination [ $\text{adjusted } R^2 = 1 - (\text{MS}_{\text{residual}})/(\text{MS}_{\text{corrected}})$ ] and the standard errors of the residual mean squares ( $\text{SE}_{\text{residual}} = \sqrt{\text{MS}}$ ) (Sit and Poulin-Costello 1994).  $\text{SE}_{\text{residual}}$  can only be used for comparisons among the nonlinear models because of scaling problems when these models are compared with the log-transformed model.

### Testing the models

Three data sets, all from seed orchards, were available to test the models. The first set (20 data points) was combined from Tables 2 and 4 in Wheeler and Jech (1986b) and included observations from different years and orchards, and from blocks with and without bloom delay and flower induction treatments. The values relate total annual pollen catch to filled seeds per cone.

The other two sets came from Douglas-fir and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) orchards on Vancouver Island. Values relate filled seed counts to pollen catch for 24-h periods summed over the period of female seed-cone exposure. In the Douglas-fir orchard, two replicates of 5 sets of seed-cone buds (5–10 buds per replicate) just at bud burst were selected from 15 trees in each of three phenological (early, mid, and late) classes. Receptive seed cones from each of the 5 replicated sets were exposed to open pollination conditions for different periods ranging from 4 to 12 days. The exposure duration for each of the 5 periods was the same within each of the phenological classes. In the fall, all cones were collected, and seeds were hand extracted and x-rayed to determine filled seeds per cone. Seed set values were averaged by replicate within tree and phenological class ( $N = 30$ ).

Pollen capture values were determined using a 7-day clock assembly mounted on a rotating platform originally described by Sarvas (1962) and further modified by Ebell and Schmidt (1964) and Webber and Painter (1996). PC values were expressed as pollen grains per square millimetre captured over a 24-h period. PC values from two stations were summed over the 5 exposure periods for each of the 3 phenological classes. Average PC values for each of the 5 exposure periods and 3 phenological classes (15 points) were then related to their corresponding seed set values.

For western hemlock, 20 data points obtained over a 2-year period were available from 3 orchards within the Lost Lake Seed Orchard complex (S. Joyce, personal communication 1994). PC values were recorded daily using a vertical tape and dowel method. Double-sided tape was wrapped around a wooden dowel (about 1.5 cm diameter) mounted about 20 cm below a sheet metal cap for protection against rain. The tape was exposed for a 24-h period (08:00 to 08:00). Pollen grains per square millimetre were counted for each of the 4 cardinal directions and then summed to represent daily pollen catch for that station. In the fall, a subsample of 10 cones from each of 8 clones near each of 20 monitoring stations was used to estimate half-cone seed counts. Mature cones were sliced in half and number of exposed seeds with embryos were counted. PC values for the receptive periods of the 8 clones and their respective half-cone seed counts were then averaged. This was done for each of the 20 stations or data points ( $N = 8$ , i.e., a data point is the mean of 8 clones around a monitoring station).

In using the data from Wheeler and Jech (1986b) we considered the possible confounding effects of data points collected over such a wide variety of conditions and treatments. While these factors can influence both temporal and spatial distribution of pollen, we hypothesized that they should not affect the basic relationship between PC and seed yield. We also considered the possible confounding effects associated with the use of different pollen capturing devices in different orchards and of interspecific differences in pollination mechanisms. Ultimately, we hypothesized that while the magnitude of the observed values might be influenced by pollen capturing devices and species, a good model of the biological relationship between PC and seed yields within devices and species should not be affected.

**Table 1.** Comparison of five models describing the relationship between pollen capture (grains/mm<sup>2</sup>) and seed yields (filled seeds per cone for Douglas-fir (Df); filled seeds per half cone for western hemlock (Hw)).

Data sets	Coefficients			$R^2_{adj}$ *	SE <sub>residual</sub> †
	<i>a</i>	<i>b</i>	<i>c</i>		
<b>Model 1: power (linear, log transformed)</b>					
Df Wash.	2.43	0.170		0.761	0.108
Df Vancouver I.	1.80	0.819		0.823	0.351
Hw Vancouver I.	0.596	0.315		0.832	0.156
<b>Model 2: power (nonlinear)</b>					
Df Wash.	11.12	0.182		0.762	2.45
Df Vancouver I.	12.45	0.456		0.687	6.72
Hw Vancouver I.	1.90	0.291		0.769	0.466
<b>Model 3: exponential</b>					
Df Wash.	26.90	-4.900		0.592	3.21
Df Vancouver I.	41.19	-1.704		0.776	5.68
Hw Vancouver I.	3.80	-0.733		0.715	0.517
<b>Model 4: logistic</b>					
Df Wash.	39.82	0.262	0.008	0.765	2.44
Df Vancouver I.	34.00	2.374	0.994	0.718	6.37
Hw Vancouver I.	3.71	0.751	0.624	0.806	0.426
<b>Model 5: negative exponential</b>					
Df Wash.	25.28	0.100		0.457	3.70
Df Vancouver I.	36.72	0.307		0.755	5.94
Hw Vancouver I.	3.62	0.601		0.752	0.482

Note: The three data sets are from seed orchards of Douglas-fir in western Washington (Wheeler and Jech 1986b), Douglas-fir on Vancouver Island, and western hemlock on Vancouver Island. Equations for the models and information on sampling procedures are given in the text.

\*Because the models had different numbers of parameters, the coefficients of determination are given as  $R^2_{adj}$ , calculated as  $R^2_{adj} = 1 - (MS_{residual}) / (MS_{corrected})$ .

†SE<sub>residual</sub> =  $\sqrt{MS}$  is an estimate of the error of prediction of *Y* for any *X*. It can be used for comparisons among models 2–5, but not with model 1, which is log transformed.

## Results

Adjusted coefficients of determination for the log–log transformed power function and for the four nonlinear models are given in Table 1. Plots of the functions are presented in Figs. 1 and 2. To some extent the fits of the data sets to the models varied with data set and model, which indicates that the choice of model may vary with data set. However, for the three data sets that we used, the log–log transformed power function gave the highest, or nearly highest, and the most consistent adjusted coefficients of determination in spite of the fact that this model lacks an asymptote. With two exceptions all models gave quite good fits to all three data sets. The exceptions are the exponential and negative exponential models for the data set from Washington, presumably because these models are strongly curvilinear and this data set lacks both low and asymptotic PC values.

## Discussion

Both biological and pollen sampling factors can influence data quality, data variability, and fit to the model. No matter how much pollen is applied, and irrespective of whether it is hand applied or wind deposited, usually 10% to 40% of the seeds are

empty at maturity (Dahms and Barrett 1975; Johnsson 1976; Owens et al. 1981, 1991; Kärkkäinen 1994). Several explanations have been proposed (Kärkkäinen 1994). Niklas and Paw U (1983) stated that the morphology or structure of the conifer seed cone, because of its effect on wind currents, aids pollen distribution within the conelet. Nonetheless, Sarvas (1962) observed that even in years of abundant flowering, when top catch values exceeded 20 grains/ovule, 4% of the ovules still were without pollen, and that PC is greater on the windward side. Orientation of the cone bud relative to the twig also influences pollen capture (Sarvas 1962). Differences among species in the slope of the PC – seed set relationship also may be due to interspecific differences in the pollination mechanism (Tomlinson 1994). Finally, factors such as ovule abortion and embryo degeneration can substantially reduce seed set of pollinated ovules (Owens et al. 1991). The last factors cannot be moderated by sampling procedure, but they increase the sampling error for seed set.

For the relationship to hold, pollen monitoring or sampling has to reflect the relative PCs at the seed cone. Differential phenology and nonuniform pollen flow within the orchard will affect the PC among trees and even among seed-cone buds within trees. Also, the capturing efficiencies of various pollen sampling devices will affect the values and accuracy of PC estimates at any particular station (Raynor 1979; Pulkkinen 1994; J.E. Webber, personal observations).

Given these potential problems, it is encouraging that the models relate seed set to PC as well and as consistently as they do. Physical theory indicates that sampling efficiency of differently shaped and sized objects varies (Gregory 1973). In our Vancouver Island examples, the trapping of western hemlock pollen used the tape and dowel method, whereas for Douglas-fir, 7-day recorders (Webber and Painter 1996) were used. In addition the pollination mechanisms of the two species differ (Owens et al. 1981; Owens and Blake 1983; Colangeli and Owens 1989). It is not expected that different samplers would capture the same number of grains, nor would they likely capture the same number for different pollen types. However, the similarity of results reported here suggests that although the efficiency of the samplers may vary, they apparently do so in a way that reflects a simple and quite consistent multiple of what is captured by the seed cone.

Recommendations for future trials relating PC and seed set would be that different sampling devices be compared side by side under a variety of conditions or treatments in order to determine whether sampling error could be influenced by choice of device. Also, where appropriate to the purposes and possibilities of the study, more sampling should be done at the low end of PC. The latter is important because the PC – seed set curve is so steep at low values of PC.

## Implications for seed orchard management

If the slope *b* in the logarithmic relationship is less than one, as it was in our examples, an increase in PC will be accompanied by a less than proportional increase in seed set. This implies that a relatively low PC, compared with that sampled during maximum pollen flight, can still result in substantial seed production. The best example of this was in the western hemlock orchard, where a pollen catch of 10 grains/mm<sup>2</sup> was associated with 3.3 filled seeds/half cone and a pollen catch of only 1 grain/mm<sup>2</sup> with 1.8 filled seeds/half cone (Fig. 1C).

Fig. 1. Relationships between seed set and estimated pollen capture for seed orchards of Douglas-fir in western Washington (A), Douglas-fir on Vancouver Island, British Columbia (B), and western hemlock on Vancouver Island (C). Plotted lines show fits to log-log transformed power functions. Additional details are given in the text.

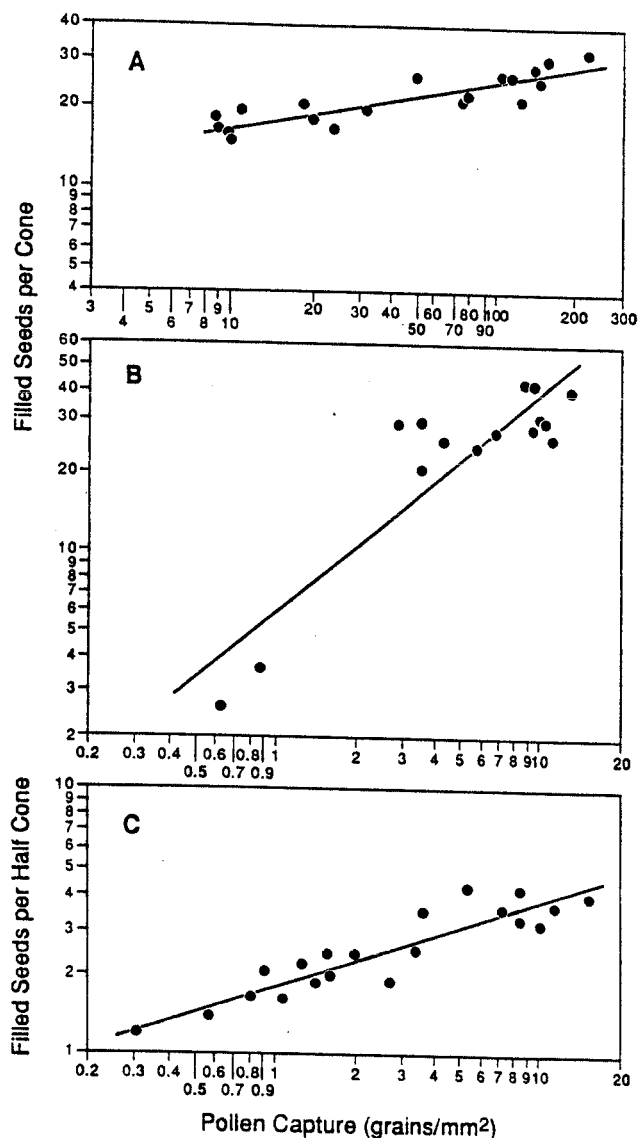
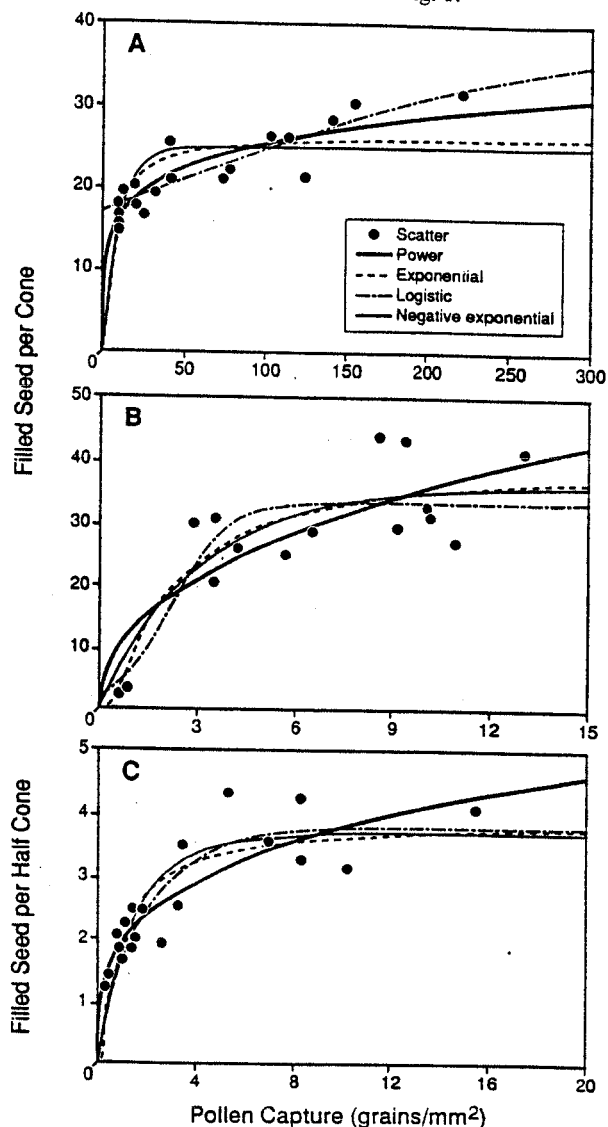


Fig. 2. Relationships between seed set and estimated pollen capture for seed orchards of Douglas-fir in western Washington (A), Douglas-fir on Vancouver Island, British Columbia (B), and western hemlock on Vancouver Island (C). Plotted curves show fits to four nonlinear models: exponential, logistic, power, and negative exponential. Data points are the same as in Fig. 1.



From a seed orchard management standpoint, the fact that relatively low PC gives substantial seed set implies that unless foreign pollen can be blocked out (controlled pollination), the origin of the first pollen to arrive is of particular importance. If the first pollen is contaminant pollen, a high rate of pollen contamination is likely even though the amount arriving might not be large (Nilsson 1995). This importance is even greater for species like Douglas-fir, which has a pollen mechanism that favors early arriving pollen (Webber and Yeh 1987). These are points that many orchard managers have learned from experience and are in agreement with the models.

The logarithmic relationship with  $b < 1$  also means that once an intermediate amount of pollen has arrived, the application of large additional amounts of pollen will be relatively ineffective in boosting seed set. For example, the relationship

in Fig. 1A for the Washington seed orchard shows that doubling the seasonal pollen catch from 50 to 100 grains/mm<sup>2</sup> increased the calculated filled seeds per cone only from 22.6 to 25.5 (by 13%). That is, once PC approaches the asymptote, which can occur at moderately low PC (Fig. 2), application of more pollen may alter male parentage somewhat but it will have only a minor effect on seed yield (Wheeler and Jech 1986a).

#### Implications for population biology

Although the PC – seed set relationship was tested using seed orchard data, observations from natural stands (see Introduction) also seem to substantiate the main features of the models. Below, we draw attention to two implications of the models for

population biology, but recognize that the comments are speculative.

The first point has to do with natural selfing and the steep part of the curve. Sorensen (1982) presented data that indicated a high incidence of natural self-fertilization (averaging 40–50% and ranging up to almost 90% for individual trees) in coastal Douglas-fir. Considering that self-pollen comes from only single individuals surrounded by extensive stands, the estimates seemed almost unbelievably high. We now suggest that these observations may be additional evidence for the high seed set (or fertilizing) potential of low PC values if the pollen arrives early in seed-cone receptivity. The amount arriving early would not have to be large relative to the total pollen cloud that the tree would ultimately receive in order to be effective in fertilization. Both proximity (pollen cone – seed cone separation in the crown) and timing (protandry (pollen cones already shedding pollen when seed cones first become receptive) vs. protogyny) would influence the potential for early self-pollination. Spatial separation and pronounced protogyny would have the effect of reducing self-fertilization and self seed set even in a relatively self-fertile species.

The second place where experimental observations from natural stands seem to substantiate the model relates to the asymptotic or near asymptotic part of the curve. In forest management, regeneration harvests remove part of the mature stand and leave varying numbers of trees for natural regeneration. The effect of the partial cuts on mating system parameters appears to be relatively small or absent (Woods and Blake 1981; Neale 1985; Neale and Adams 1985). Similarly, within broad limits both density of natural stands (Furnier and Adams 1986) and species frequency in mixed stands (Sorensen 1994) seem to have a relatively slight effect on mating system estimates. Smith et al. (1988) found significant change in frequency of filled seeds per cone across a nearly 50-fold range in stand densities of lodgepole pine, but the change in seed set (61% to 88% filled) was small compared with the change in stand density. Other factors such as pollen production per tree can be important (Smith et al. 1988), but if comparatively low stand densities or species frequencies still have PC levels approaching the asymptotic part of the curve, estimated seed sets and perhaps mating system parameters should not differ greatly from similar estimates made in stands of much higher density.

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## References

- Bramlett, D.L. 1977. Pollen quantity affects cone and seed yields in controlled slash pine pollinations. *Proc. South. For. Tree Improve. Conf.* 14: 28–34.
- Bramlett, D.L., and O'Gwynn, C.H. 1981. Controlled pollination. *In* Pollen management handbook. *Edited by* E.C. Franklin. U.S. Dep. Agric. Agric. Handb. 587. pp. 44–51.
- Colangelo, A.M., and Owens, J.N. 1989. Postdormancy seed-cone development and the pollination mechanism in western hemlock (*Tsuga heterophylla*). *Can. J. For. Res.* 19: 44–53.
- Dahms, W.G., and Barrett, J.W. 1975. Seed production of central Oregon ponderosa and lodgepole pines. *USDA For. Serv. Res. Pap. PNW-191*.
- Di-Giovanni, F., and Kevan, P.G. 1991. Factors affecting pollen dynamics and its importance to pollen contamination: a review. *Can. J. For. Res.* 21: 1155–1170.
- Ebell, L.F., and Schmidt, R.L. 1964. Meteorological factors affecting conifer pollen dispersal on Vancouver Island. *Can. Dep. For. Publ.* 1036.
- El-Kassaby, Y.A., Barnes, S., Cook, C., and McLeod, D.A. 1993. Supplemental mass pollination success rate in a mature Douglas-fir seed orchard. *Can. J. For. Res.* 23: 1096–1099.
- Furnier, G.R., and Adams, W.T. 1986. Mating system in natural populations of Jeffrey pine. *Am. J. Bot.* 73: 1002–1008.
- Gregorius, H.-R. 1983. Efficiency of random pollination and optimal sex ratio. *Math. Biosci.* 66: 263–271.
- Gregory, P.H. 1973. *The microbiology of the atmosphere*. 2nd ed. Leonard Hill, Aylesbury, England.
- Harris, A.S. 1969. Ripening and dispersal of a bumper western hemlock – Sitka spruce seed crop in southeast Alaska. *USDA For. Serv. Res. Note PNW-105*.
- Johnsson, H. 1976. Contributions to the genetics of empty grains in the seed of pine (*Pinus silvestris*). *Silvae Genet.* 25: 10–15.
- Kärkkäinen, K. 1994. Why does Scots pine abort so many of its seeds and cones? *In* Deleterious mutations and sexual allocation in evolution of reproduction of Scots pine. Dissertation, University of Oulu, Oulu, Finland. Acta A259, original paper V.
- Neale, D.B. 1985. Genetic implications of shelterwood regeneration of Douglas-fir in southwest Oregon. *For. Sci.* 31: 995–1005.
- Neale, D.B., and Adams, W.T. 1985. The mating system in natural and shelterwood stands of Douglas-fir. *Theor. Appl. Genet.* 71: 201–207.
- Niklas, K.J., and Paw U, K.T. 1983. Conifer ovulate cone morphology: implications on pollen impaction patterns. *Am. J. Bot.* 70: 568–577.
- Nilsson, J.-E. 1995. Genetic variation in the natural pollen cloud of *Pinus sylvestris*: a study based on progeny testing. *Scand. J. For. Res.* 10: 140–148.
- Owens, J.N., and Blake, M.D. 1983. Pollen morphology and development of the pollination mechanism in *Tsuga heterophylla* and *T. mertensiana*. *Can. J. Bot.* 61: 3041–3048.
- Owens, J.N., and Blake, M.D. 1985. Forest tree seed production: a review of the literature and recommendations for future research. *Can. For. Serv. Petawawa Natl. For. Inst. Inf. Rep. PI-X-53*.
- Owens, J.N., Simpson, S.J., and Molder, M. 1981. The pollination mechanism and the optimal time of pollination in Douglas-fir (*Pseudotsuga menziesii*). *Can. J. For. Res.* 11: 36–50.
- Owens, J.N., Coangelo, A.M., and Morris, S.J. 1991. Factors affecting seed set in Douglas-fir (*Pseudotsuga menziesii*). *Can. J. Bot.* 69: 229–238.
- Pulkkinen, P. 1994. Aerobiology of pine pollen: dispersal of pollen from nonuniform sources and impact on Scots pine seed orchards. *Rep. Found. For. Tree Breed. (Helsinki)*, No. 8.
- Raynor, G.S. 1979. Sampling techniques. *In* Aerobiology: the ecological systems approach. *Edited by* R.L. Edmonds. Dowden, Hutchinson and Ross, Stroudsburg, Pa. pp. 151–172.

- Sarvas, R. 1962. Investigations of the flowering and seed crop of *Pinus silvestris*. Commun. Inst. For. Fenn. 53.4.
- Silen, R.R. 1979. Genetics of Douglas-fir. U.S. For. Serv. Wash. Off. Res. Pap. WO-35.
- Sit, V., and Poulin-Costello, M. 1994. Catalogue of curves for curve fitting. British Columbia Ministry of Forests, Research Program, Victoria. Biometrics Inf. Handb. 4.
- Smith, C.C., Hamrick, J.L., and Kramer, C.L. 1988. The effects of stand density on frequency of filled seeds and fecundity in lodgepole pine (*Pinus contorta*). Can. J. For. Res. 18: 453-460.
- Sorensen, F.C. 1982. The roles of polyembryony and embryo viability in the genetic system of conifers. Evolution, 36: 726-732.
- Sorensen, F.C. 1994. Frequency of seedlings from natural self-fertilization in Pacific Northwest ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.). Silvae Genet. 43: 100-108.
- Sorensen, F.C., and Adams, W.T. 1993. Self fertility and natural selfing in three Oregon Cascades populations of lodgepole pine. *Pinus contorta*—from untamed forest to domesticated crop. Edited by D. Lindgren. Swed. Univ. Agric. Sci. Dep. For. Gen. Plant Physiol. Rep. 11: 358-374.
- Sorensen, F.C., Franklin, J.F., and Woollard, R. 1976. Self pollination effects on seed and seedling traits in noble fir. For. Sci. 22: 155-159.
- Squillace, A.E. 1967. Effectiveness of 400-foot isolation around a slash pine seed orchard. J. For. 65: 823-824.
- Tomlinson, P.B. 1994. Functional morphology of saccate pollen in conifers with special reference to Podocarpaceae. Int. J. Plant Sci. 155: 699-715.
- Webber, J.E. 1995. Pollen management for intensive seed orchard production. Tree Physiol. 15: 507-514.
- Webber, J.E., and Painter, R.A. 1996. Douglas-fir pollen management manual: 2nd ed. British Columbia Ministry of Forests, Research Branch, Victoria. Work.Pap. 02/1996.
- Webber, J.E., and Yeh, F.C.H. 1987. Test of the first-on, first-in pollination hypothesis in coastal Douglas-fir. Can. J. For. Res. 17: 63-68.
- Wheeler, N.C., and Jech, K.S. 1986a. Estimating supplemental mass pollination (SMP) success electrophoretically. In New Ways in Forest Genetics. Proceedings of the Canadian Tree Improvement Association. 20 (part 2), 19-22 Aug. 1985, Québec. Canadian Forestry Service, Ottawa. Edited by G.E. Caron, A.G. Corriveau, and T.J.B. Boyle. pp. 111-120.
- Wheeler, N.C., and Jech, K.S. 1986b. Pollen production and contamination in Weyerhaeuser's Douglas-fir seed orchards. Weyerhaeuser Co., Centralia, Wash. Res. Tech. Rep. 050-3210/14.
- Woods, J., and Blake, G. 1981. The effect of seed tree regeneration systems on the genetic diversity of ponderosa pine. In Progress Report of the Inland Empire Tree Improvement Cooperative, Aug. 1981. Prepared by L. Fins. University of Idaho, Moscow.