Limitations of pollen management strategies for southern pine seed orchards

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Seed orchard pollen management can range from passive types such as careful arrangement of trees to encourage a uniform mixing of clones throughout the orchard to collecting pollen and artificially pollinating bagged female strobili. The general goals are the same for both extremes. Desirable crossing patterns are being encouraged and undesirable matings are being minimized.

In production orchards, estimation of the orchard's genetic potential is based on anticipated mating proportions. The assumption that all clones contribute equal pollen proportions to the seed crop is often used in wind-pollinated seed orchards. If pollen strobilus production varies among the orchard clones, a weighted average for the pollen contributions might be used. Also, production orchards typically include a buffer zone or pollen dilution zone which is used to minimize the proportion of matings that occur with non-selected or foreign pollen. The undesirable pollen may arise from trees of a like species with the orchard or from trees that will readily hybridize with the orchard species.

In breeding orchards, mating types and proportions are often managed by controlled pollination. That is, protecting the female strobili from unwanted pollen and then introducing a pollen source that has been selected for the specific mating. In both orchard types it may be desirable to augment standard pollen management practices with supplemental mass pollination (SMP) if unprotected strobili are being pollinated. Selected pollen may be mist blown throughout the orchard or applied directly to the strobilus. With all pollen management systems in all orchard types the goal is to focus the pollination process on specific desired matings.

Goals represent ideal situations. If all aspects of orchard management are exact and predictable, the goals will be met. However, as in any natural system, all practices are rarely exact and often unpredictable.

DEVIATIONS FROM AN IDEAL ORCHARD

A. POSITIONING

Establishing the geographic layout of a clonal seed orchard is usually a complicated task. First generation orchards may have as many as 150 clones with as many as 50 ramets per clone. Individual trees need to be placed in a pattern that will allow equal opportunity of cross-pollination among all clone pairs and minimum opportunity for selfing between ramets of the same clone. A minimum distance rule such as the 90-foot rule is often applied to the orchard. In this case, no two ramets of the same clone will be positioned any closer than 90 feet from each other. Placement of clones throughout the orchard may be a random process or a systematic process.

In the rare orchard where all trees produce equal amounts of male and female strobili and flowering is completely synchronized among all of the clones, a carefully constructed layout may allow for equal mating proportions among the different clones. If all ramets from a common clone are separated by sufficient distance, inbreeding may be effectively eliminated. However, mot orchards suffer from one or more deviations from the ideal situation.

Orchard roguing, graft incompatibility and other problems may cause the original placement scheme to be altered. As a result of these changes, some clones will have more ramets than others and the relative positioning will be far from the desired format.

Average distance between clones is not a good indicator of the potential for uniform pollen dissemination. Pollen flight probabilities usually follow an exponential distribution with increasing distance from the source tree. Tree pairs that are close together receive a disproportionately large share of the pollen than tree pairs separated by greater distances. Random positioning of trees should provide mathematically similar cross-pollination probabilities if sufficient numbers of ramets from each clone are used to minimize small sampling errors.

Systematic designs, in general, tend to group clones in similar patterns and severely limit interclone matings. However, a systematic design based on environmental factors and measured phenological and physiological characteristics of the trees may result in an ideal cross-pollination pattern.

B. FLOWERING PHENOLOGY

Flowering differences among clones occurs in all orchards and in some cases the variation is great enough to eliminate any possibility of equal or predictable representation among the clones. Variation in female strobilus production and male strobilus production on a given tree coupled with variation in times of receptivity and pollen flight may eliminate the possibility of desired mating types and severely skew the distribution of realized mating types away from a uniform distribution. Variation in female strobilus production is an inherent problem for pollen management in that it causes clonal differences in ability to receive pollen. A clone that is prolific in female strobilus production can certainly acquire more pollen than a clone with poor female strobilus productivity. Phenology variation coupled with placement problems can render genetic estimation of the seed crop almost impossible and at least destroy the precision and accuracy of the genetic estimates.

Disproportionate flowering or poor synchronization among clones is probably :he largest single factor that affects the cross-pollination patterns in seed orchards. Problems discussed by Askew (1986), Blush (1986), El-Kassaby et al (1988), and others demonstrate the potential for complete exclusion of some clones from the pollen pool and the isolation of some seed parents from the orchard produced pollen. Using more ramets from low pollen production clones and reducing the representation of the high pollen production clones may help to alleviate the problem but the best tactic may be to carefully monitor the orchard phenology and to construct an orchard of synchronous clones as part of the roguing process.

Orchards with severe phenology problems need to have both the flowering characteristics as well as the seed production characteristics and genetic testing results incorporated into the selection process.

C. INSECT PREDATION

Insect predation of cones and seeds is another inherent problem that needs to be considered during pollen management development. Insect predation can eliminate as much as 90% of a trees cone crop and variation in predation rates among clones has been documented in several orchards (Askew et al 1985 a & b). Seed and cone insects can be major factors in determining the genetic composition of a seed crop and can alter the pollen contribution percentages as well as the seed contribution percentages. If a uniform pollen pattern is acquired but seeds are eliminated from the crop in a non-random or non-uniform pattern, the pollen contribution distribution is also effectively skewed. In fact, in orchards where the pollen contributions vary within the seed crops of individual clones, the alteration of gamete contribution proportions due to insects will vary greatly between the pollen parent and the seed parent. Pest management practices may be costly and monitoring programs are often necessary to keep abreast of the damage and the effectiveness of the treatment.

D. PREVAILING WINDS

Orchards that are established in areas with prevailing winds at the time of pollen dissemination have a severe handicap. Downwind trees will certainly contribute less pollen to the seed crop than upwind clones. Buffer strips that are used as fall-out areas for pollen produced by neighboring trees need to be much wider on the upwind side of the orchard and may be of minimal value on the downwind side. Relative clone positioning throughout the orchard will need to be based on pollen dissemination distributions that are not uniform around the individual trees but are skewed toward the downwind side.

Pollen distribution patterns that are skewed by prevailing winds will severely affect the accuracy of the genetic evaluation techniques. Positioning of individual trees in a systematic design must be based on prevailing wind factors if pollen dissemination patterns are to be maintained at a desired level. Freeman (1967) suggested the use of balanced incomplete block designs to address this problem. Other designs such as random placement may be less susceptible to large deviations due to wind than a systematic design but will still be impacted by heavier foreign pollen doses on the upwind side of the orchard. It is imperative that poor pollen producers be shifted upwind relative to the heavy producers. Likewise, high quality clones should be positioned so the majority of their pollen falls within the orchard.

Monitoring studies are warranted for any orchard impacted by prevailing winds in order to quantify the degree of pollen drift and variation in wind direction and velocity during the pollination season.

E. POLLEN QUALITY

If variation in pollen viability or germination rate exists among the orchard clones, getting the pollen to the ovule will not assure the desired fertilization proportion. Instead, poor quality pollen sources will need to have greater pollen grain representation than high quality sources in order to boost the probability of attaining the desired fertilization percentages.

All orchards need to be tested on a regular basis to identify any severe variation in pollen viability. Orchard management practices can be altered or supplemental mass pollination may be implemented to alleviate low pollen potential in desired clones.

F. ADVANCED GENERATIONS

Advanced generation orchards may contain all of the problems of the first generation orchards plus an added problem. Almost certainly, the second or third generation selections will have higher coancestry levels than the first generation orchard. Relatedness among ramets that was the only source of inbreeding in the first generation orchard will be joined by relatedness among the clones. Full-sib and half-sib relationships could easily exist as could cousin and perhaps double cousin relationships. If inbreeding is to be avoided or minimized, additional placement constraints will be necessary. These constraints may exacerbate the problems of accommodating variation in phenology, pollen quality, insect predation and impacts of prevailing winds.

Selecting parent trees for advanced generation orchards solely on the basis of metric values to the exclusion of breeding characteristics may affect the realized genetic potential of the orchard. Monitoring studies of potential parents prior to selection would be useful to establish heritability of breeding traits and selection of phenologically conpatible trees will facilitate efficient cross-pollination and genetic balance.

G. SUPPLEMENTAL MASS POLLINATION

Pollen supplementation methods such as SMP can be effective only when the orchard manager has a complete understanding of his orchard phenology and other pollen management problems. Timing of SMP treatments may need to be tailored to individual clones or perhaps individual trees in higher generation orchards. The amount of genetic improvement to be attained by SMP is a function of the degree of replacement of undesirable pollen with desirable pollen and the differential of the ambient pollen clouds value and the SMP value. The problems mentioned earlier can cause great variation in the day-to-day value of the ambient pollen cloud and hence the degree of genetic improvement that is possible will vary from day-to-day. If severe variation exists in mating proportions, SMP might be needed to assure a high quality seed crop and may actually dominate the pollination percentages. If SMP is used in such an intensive manner as to effectively replace wind pollination within the orchard, then the SMP pollen composition needs to assure genetic diversity as well as genetic improvement. A program that utilizes only a few pollen sources for productions of millions of seeds would be questionable unless the genetics of the system were well known and GxE problems were not anticipated.

ESTIMATION OF GENETIC VALUES

All of the environmental and physiological limitations to pollen management can be accounted for in a mathematical estimation procedure. If quantitative data is lacking for a particular factor, the coefficients can be set at a conservative value until the data is gathered. Any number of estimation procedures are possible, but a simplified, straightforward approach is recommended here.

The average genetic value of seeds collected from clone j (Sj) in an orchard containing n clones is calculated as:

$$S_j = \frac{1}{2}\left(\left(\sum_{i=1}^{n} P_{ij} \cdot GV_i\right) + GV_j\right) \qquad (1)$$

where Pi• is the proportion of seed produced by clone i pollinating clone j and GV i the genetic value of clone i or j. Pij is calculated as:

$$P_{ij} = \frac{PM_{ij}}{\sum_{i=1}^{n} PM_{ij}} \qquad (2)$$

where PM$_i$j is the relative probability of clone i pollinating clone j given flowering phenologies, pollen production levels, and pollen viability (after Askew 1988).

The genetic value of the orchard crop (GVO) realized by nursery production of seedlings from orchard seed is:

$$GVO = \sum_{j=1}^{n} \frac{S_j \cdot I_j \cdot V_j \cdot SP_j}{\sum_{j=1}^{n} I_j \cdot V_j \cdot SP_j} \qquad (3)$$

where I$_j$ is the insect predation survival rate of clone j's seed crop; Vj is the germination percentage of clone j's seed crop; and SP$_j$ is clone j's female strobilus production value.

In effect,

$$\frac{I_j \cdot V_j \cdot SP_j}{\sum_{j=1}^{n} I_j \cdot V_j \cdot SP_j} \qquad (4)$$

is the proportion of the orchards seedlings produced from seed of clone j.

It is interesting to note that of all of the factors that can influence the final genetic composition of the seed crop, only S_j is generally measured in most seed orchards.

Harvest proportions, after insect predation, can be calculated as:

$$I_j \cdot SP_j$$

Each factor should be specified at the outset of any orchard analysis and removed from the equations if it is found to be unimportant. Disregarding all of the potential limiting factors during the development of a pollen management strategy or in the process of roguing or design may lead to erroneous estimations of genetic value.

PMij is developed by studying strobilus production rates and flowering phenology for each clone. It may be based on several years of observation or recalculated for each season. Flowering induction techniques, supplemental mass pollination, orchard design and roguing will affect the value of PMij.

I_j may be estimated by insect damage surveys during cone harvesting. Insect control measures will affect the value of I and yearly fluctuations among individual clones should be expected.

Vj (seed viability) is usually not a problem in most orchard systems. However, in some instances sufficient variation may exist among individual seed lots to warrant its inclusion in genetic estimates. V's may be affected by seed handling techniques, orchard practices or vary due to inherent genetic variation and therefore it is a factor that may influence pollen management decisions.

SP_j is an important factor to monitor for orchard planning and genetic estimation. Final seed counts may be affected by a number of environmental factors that are either controllable or totally uncontrollable and unpredictable. In either case, it is important to have an understanding of the seed production potential of each clone in the absence of the modifying factors.

Overall, every variable is subject to modification either by natural fluctuations in the environment or by directed changes brought about by orchard management practices.

One final factor that affects the relative importance of the factors that influence the genetic value of the seed crop and the pollen management strategies is orchard size. Orchards with large numbers of clones (> 50) will generally be more stable in the presence of phenological or physiological variation among the clones. In effect, each clone in a 50 clone orchard is expected to contribute only 2% of the gametes and only very large variations in gamete contributions affecting many clones will cause an appreciable change in the overall genetic structure of the seed crop. Small orchards (<20 clones) are more susceptible to wide swings in genetic constitution. Significant changes in the gamete contributions of only 2 or 3 clones can greatly upset the distribution. Size acts as a buffer to clonal variation with respect to expected genetic values. The principle is similar to the problems of genetic drift and other small sample problems.

SUMMARY AND CONCLUSIONS

Pollen management strategies need to accommodate variation among clones in cone and seed insect susceptibility, gamete production, flowering phenology, seed and pollen viability and other factors that affect the final genetic omposition of the seed crop. Orchard design, prevailing winds and other environmental factors must also be considered during the planning of any management tactic or during the estimation of genetic value.

Accurate estimation of the final genetic composition of a seed crop will allow for effective planning for pollen management or supplementation. Orchard designs and parental selections can be used to minimize undesirable genetic problems and help the manager produce a consistent, predictable genetic composition.

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