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Quantifying Uniformity of Gamete Production in Seed Orchards

By G. R. ASKEW

Belle W. Baruch Forest Science Institute
of Clemson University[1])

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Summary

Genetic uniformity of seed orchards is often discussed in subjective terms such as asymmetry of gamete production, pollen contamination levels, etc. A quantitative index of orchard uniformity, U, that integrates gamete production and foreign pollen contamination is proposed. This index provides forest geneticists with a quantitative method of comparing orchards or evaluating changes in annual production of a single orchard. Index calculation requires estimates of microspore and megaspore production levels for individual clones and an estimate of the degree of pollen contamination.

Key words: variance, strobili, gamete production.

Zusammenfassung

Die genetische Einheitlichkeit von Samenplantagen wird oft unter einseitigen Gesichtspunkten wie z. B. der Asymmetrie der Gametenproduktion, dem Pollenkontaminations-Niveau usw. diskutiert. Ein quantitativer Index für die Plantagenuniformität, U, der die Gametenproduktion und die Fremdpollenkontamination miteinbezieht, wird vorgeschlagen. Der Index versorgt die Forstgenetiker mit einer quantitativen Methode, Samenplantagen zu vergleichen oder Unterschiede in der jährlichen Produktion einer einzelnen Plantage zu errechnen. Eine Index-Berechnung erfordert Schätzungen des Mikro- und Megasporen-Produktionsniveaus der Einzelklone und eine Schätzung des Grades der Pollenkontamination.

Introduction

Success or failure of a tree improvement program is largely dependent on the breeders' ability to identify genetically superior trees and to use them to produce progeny that out-perform trees derived from unimproved sources. A program's success can be measured by the realized level of improvement in the progeny and more specifically by the realized genetic gain. Improvement programs for many coniferous tree species rely on wind-pollinated seed orchards for large-scale seed production efforts. The value of these seed orchards is a function of their total seed yield and the realized genetic gain of their seeds.

Realized genetic gain is often calculated as a deviation of progeny test scores from a checklot (TALBERT, *et al.* 1985) rather than by comparing the checklot to trees grown from bulk samples of seed orchard seed. Estimation of realized genetic gain in seed orchard seed using progeny test data is often based on the assumption of uniformity of gamete contributions among clones. Complete genetic uniformity requires several conditions: a) equal production of microspores and megaspores by each clone in the orchard; b) equal viability of microspores and megaspores; c) synchronized production of microspores and megaspores; d) random union of gametes among all non-related pairs of clones and e) negligible levels of alien pollen. Several studies have documented variation in microspore and megaspore production and effectiveness (BERGMANN 1968, MÜLLER-STARCK 1982, SCHMIDTLING 1983) by use of field counts of flowers and electrophoretic studies of seed. Field counts of male and female flowers can serve as rudimentary estimates of potential gamete contributions and electrophoretic analysis of bulk seed lots may enable breeders to quantify the actual gamete contributions of each clone to the final seed crop. Variation in gamete production needs to be incorporated into the calculation of genetic gain or erroneous estimates will be obtained.

Orchards that vary from the assumptions stated above are said to be less uniform but uniformity is usually described in subjective terms that specify the degree of departure from optimum productivity. Such subjectivity makes it difficult to compare the annual productivity of a single orchard or to compare productivities among several orchards. The purpose of this paper is two-fold. First, to

[1]) P. O. Box 596, Georgetown, S. C. 29442, USA

examine the effect of non-uniform microspore and megaspore production among clones on the distribution of total potential gamete contributions and second, to propose a measure of seed orchard genetic uniformity based on the variance in proportional gamete production.

Estimator Development

Clonal contributions can be characterized by the distribution of proportions of gametes produced by each clone. The sum of the proportions is unity. Both the microspore and megaspore contributions will be characterized in this manner. The estimator of seed orchard genetic uniformity is developed as follows.

Let the variance of microspore proportions among clones equal σ^2_m and the variance of megaspore proportions equal σ^2_f. If gametes are paired at random the variance of total gamete proportions σ^2_g is:

$$\sigma^2_g = \frac{\sigma^2_m + \sigma^2_f}{4} + \rho \frac{\sigma_m \sigma_f}{2} ; \qquad (1)$$

where p is the correlation of microspore and megaspore proportions. The maximum value of σ^2_g is:

$$\sigma^2_{g\,max} = \frac{(n-1)}{n^2} \qquad (2)$$

where n is the number of clones in the orchard. $\sigma^2_{g\,max}$ occurs when one clone produces all of the microspores and all of the megaspores and therefore p = 1. This would rarely occur but serves as a baseline for viewing the degree of variance denoted by σ^2_g. Orchard uniformity, U, can then be expressed as:

$$U = 100\ (1 - (\sigma^2_g/\sigma^2_{g\,max})). \qquad (3)$$

Friedman and Adams (1981) examined the degree of pollen contamination in two loblolly pine seed orchards. They concluded that pollen contamination "may be the single most important factor in reduction of genetic uniformity". Sniezko (1981) discussed the effects of pollen contamination on gene frequencies in seed orchards and discussed recommendations offered by Squillace and Long (1981) for minimizing pollen contamination levels. These studies point to the necessity of adjusting estimates of orchard uniformity to compensate for pollen contamination. Pollen contamination is incorporated into the index as:

$$U = [(1 - C)\ (1 - (\sigma^2_g/\sigma^2_{g\,max})) + \frac{C}{2}\ (1 - (\sigma^2_f/\sigma^2_{g\,max}))]\ 100\ ; \qquad (4)$$

where C is the proportion of alien pollen. U is now composed of two parts. The proportion of matings involving orchard pollen, (1-C), will have a uniformity value that is determined as before, but the proportion of matings involving alien pollen, C, is a function of only σ^2_f and has a maximum value of 0.5 because matings that do not involve orchard pollen contain only 50% selected gametes. U still attains its maximum value when $\sigma^2_g = 0$ but only when the pollen contamination level, C, is also zero. Minimum U is still zero and occurs when C = 0 and $\sigma^2_g = \sigma^2_{g\,max}$ or when C = 1 and $\sigma^2_f = \sigma^2_{g\,max}$.

Discussion and Illustration

U was designed to utilize gamete contribution proportions instead of actual gamete counts because proportion estimation may be easier to accomplish in orchards. An examination of several ramets of each clone should be sufficient to score each clone for its relative contributions to the total gamete pool. Estimates of pollen contamination levels are not as simple to obtain and require an analysis such as electrophoresis on a bulk seed samples. The best approach would be to estimate σ^2_g from pollen and flower production and then test the effects of an array of contamination values.

Conservative estimates of U can easily be obtained from seed production records. Seed production levels of each clone can be converted to proportions and used to estimate σ^2_f. Microspore variance, σ^2_m can be assumed to be zero, equal to σ^2_f or $\sigma^2_{g\,max}$ to cover the range of possible values. These conservative estimates can be used to study the stability of U from year to year.

Pollen contamination levels, C, could have been included in the model in several ways. The most plausible approach seemed to be to consider the seed crop as two parts. One part is unaffected by alien pollen and uniformity estimates are calculated as usual. The second part of the crop is pollinated solely by alien pollen. Hence this proportion, C, of the crop contributes selected gametes from just the megaspore portion and has a maximum uniformity of 50% which occurs when $\sigma^2_f = 0$. The overall uniformity rating is a sum of the two parts, each weighted by the proportion of the total seed crop that they represent.

Correlation of proportionate male and female strobili production, denoted by p, can be either beneficial or deleterious to orchard uniformity. If $\sigma^2_m \neq 0$ and $\sigma^2_f \neq 0$ then an increasingly negative correlation will result in an increasing index value until p = −1 when U = 100. At this point, $\sigma^2_m = \sigma^2_f$ and disproportinate gamete contributions from one sex are completely compensited for by the other sex. Conversely, positive values of p cause decreased values of U. Disproportionate gamete contributions of one sex are compounded by concomitant disproportionate contributions by the other sex.

Barnes and Mullin (1974) studied male and female strobili production in 28 *P. taeda* clones. Variance in proportional productivity during weeks 31—37, the time of maximum receptivity, was $\sigma^2_f = 0.0013067$ and $\sigma^2_m = 0.0047346$. Correlation of male and female productivity was p = 0.61524. If there was no pollen contamination (C = 0) then $\sigma^2_g = 0.0022755$, $\sigma^2_{g\,max} = .0344388$ and U = 93.4. The range among clones in female strobili contributions was 0—15.4% and the range in male strobili production was 0—26.2%. If pollen contamination had been 20%, as reported in some seed orchards then U would have dropped to 84.

Variation in megaspore production has the potential to affect U more than variation in microspore production because pollen contamination will tend to dampen the effect of σ^2_m. As the pollen contamination level increases, the effect of σ^2_m decreases and σ^2_f begins to dominate U.

U values are not indicative of the fecundity of the orchard or the broadness of its genetic base, but only the uniformity of contributions. A two clone orchard in which each clone produces 50% of the gametes will have a rating of 100 as would a 100 clone orchard in which each clone contributed 1% of the gametes. Sufficiency of the orchard's genetic base must be determined by other means.

It is important to remember that U is only an estimate of the orchard's relative uniformity. That is, how close the gamete distribution is to its worst possible value. Individual breeders will need to determine the minimum acceptable level of U for their specific orchards.

Conclusion

An index that quantifies the variability in gamete contribution allows breeders to evaluate their orchard's performance and compare it to similar orchards. The index also provides breeders with a method of checking for efficacy of cultural treatments or stability of gamete production as the orchard matures.

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Buchbesprechungen

Tropical Trees and Forests — an Architectural Analysis. By HALLÉ, F., OLDEMANN, R. A. A. and P. B. TOMLINSON, XVII + 441 p., 111 Figures, 10 Tables. Springer Verlag, Berlin, Heidelberg, New York 1978.

This book is concerned with the analysis of tropical forest ecosystems in terms of their constituent units, the individual trees. With it HALLÉ (Montpellier), OLDEMAN (Wageningen), and TOMLINSON (Harvard) do not intend to give a survey of known information in the manner of a text-book, but want to present a point of view, which is supported largely by their own scientific findings.

The approach is to regard trees as genetically diverse, developing, changing individuals, which respond in various ways to fluctuations in climate and microclimate, the incidence of insects, fungal and other parasites and particularly to changes in surrounding trees. As a framework for this approach the tree species are divided into 23 developmental models according to their developmental plans and architecture. The description of these models takes up more than half of the book (p. 13—269). Recognition of the ways a tree is constructed in a natural stressed environment, as distinct from an "ideal" tree, growing precisely according to its genetic plan and not subject to environmental stress, is accomplished by "reiteration", which leads to the "opportunistic tree architecture". Reiteration is the change in the tree model which results from the intermittent growth of the tree as a response to the environmental influences.

The characteristics of a forest stand are analysed in view of "sylvigenesis" (the process by which forest architecture is being built) and "homoestasis" (a stable state of the forest). As examples for the analysis of the development of the stand structure two stands, one in French Guiana and the other in Harvard Forest (red oak-maple forest), are introduced. The text is followed by a glossary, literature, index of plant names and their models as well as reference to the place in the text where they occur, and a detailed subject index.

The book can be used without mathematical equipment since the approach has a distinct qualitative character. Also in much on the analysis of tree form and forest stands, the dimensions are not higher than four, threedimensional space plus time. This book is not a text book, but more a book which encourages to test one's knowledge. The concepts given are very useful and encourages one to think or develop new ideas in the difficult analysis of forest ecosystems. G. v. WÜHLISCH

Lehrbuch der Pflanzenphysiologie. Von H. MOHR und P. SCHOPFER. Dritte, völlig neubearbeitete und erweiterte Auflage. Springer-Verlag, Berlin, Heidelberg, New York. 1978. 608 Seiten mit 639 Abbildungen und 35 Tabellen. DM 78,—.

Seit Erscheinen des vorliegenden Lehrbuches über die Pflanzenphysiologie ist zwar schon einige Zeit verstrichen, doch soll trotz dieser Verspätung auf dieses bemerkenswerte Werk von H. MOHR und P. SCHOPFER hingewiesen werden. In verständlichem und flüssigem Stil wird hier das umfangreiche Gebiet der Pflanzenphysiologie behandelt. Die einzelnen Themen werden anhand instruktiver und überzeugender Beispiele erarbeitet. Zum Verständnis tragen die zahlreichen übersichtlichen und sich auf das Wesentliche beschränkenden Zeichnungen bei. Hervorzuheben sind die ausführlichen Erläuterungen zu den Abbildungen, wo durch sich Zusammenhänge besonders leicht erkennen lassen. Die Abbildungen wurden in einem erfreulich großzügigen Maßstab gedruckt, was neben dem übersichtlichen und gut gegliederten Druckbild wesentlich zum Lesevergnügen beiträgt. — Inhalt des Lehrbuches ist die Darstellung der Physiologie als exakte, quantitative Wissenschaft innerhalb der experimentellen Biologie. Ihre physiologisch-systemerhaltende Arbeitsrichtung ist zwar eigenständige Forschung, aber dennoch eng mit der biochemisch-analytischen Arbeitsrichtung der Biochemie verbunden. Die Physiologie hat dabei den Auftrag zu erfüllen, biologische Systeme durch quantitative Systemmodelle zu erklären. Auf die Systeme Zelle, Organ und Organismus wird in den 49 Kapiteln dieses Lehrbuches unter verschiedenen Themenstellungen ausführlich und aktuell eingegangen. Jedem Kapitel sind zur weiteren Vertiefung des Stoffes Hinweise auf neuere Veröffentlichungen angefügt. Das Buch schließt mit einem Anhang zur Erläuterung von Maßeinheiten usw., einem Literaturverzeichnis und einem ausführlichen Sachverzeichnis. Dieses Lehrbuch ist allen an der Pflanzenphysiologie Interessierten uneingeschränkt zu empfehlen.

B. R. STEPHAN

Physiological ecology of the alpine timberline. Tree existence at high altitudes with special reference to the European alps. By W. TRANQUILLINI. Ecological Studies Vol. 31. Springer-Verlag, Berlin - Heidelberg - New York. 1979. 137 p. with 67 fig. DM 54,—.

In this volume of the Springer-series "Ecological Studies" the author W. TRANQUILLINI, Innsbruck, presents a very valuable and interesting review on experimental results of ecophysiological studies at the upper timberline, especially in the Alps, but when appropriate also from other parts of the world. In the three introducing and short chapters the author describes the general features of the upper timberline, the reasons for occurrence of timberlines and their experimental investigation, and some milestones in the history of ecophysiological research concerning alpine timberline. In the six main chapters of the book emphasis has been placed on the description of the interrelationship between site factors and the most important life processes. At timberline site factors are extremely significant and become the limiting factors for vital plant processes. The following topics are dealing with the natural regeneration of tree stands at timberline, growth of trees, dry matter production, water relations and climatic resistance and damage. In the last chapter an attempt has been made to develop a general picture of the trees' life at the limit of existence in the mountains. This book gives a very fine summary about a very specific topic and can be recommended to all, who are interested in plant ecology and forestry at higher altitudes. B. R. STEPHAN

Bamboos II. By RIDOUT, L. M. Annoted Bibliography No. F 32 Comm. Agric. Bureaux, Slough SL2 3BN, UK, 1983. Price: £ 11.85, US $ 24.90.

Under 13 subject headings a collection of abstracts which entered Forestry Abstracts and other CAB journals between 1978—1982 is