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Literature cited

Buckley, D. P., O'Malley, D. M., Apsit, V. S., France, G. T. and Bawa, K. S.: Genetics of Brazil nut (*Bertholletia excelsa*, Humb. and Bonpl.; *Lecythidaceae*). 1. Genetic variation in natural populations. Theor. Appl. Genet. **76**: 923—928 (1988). —— Chevallier, M. H.: Genetic variability of *Hevea brasiliensis* germplasm using isozyme markers. Il. Rubb. Res. Inst. of Malaysia **3**: 42—53 (1988). —— Chevallier, M. H., Lebrun, P. and Normand, F.: Approach to the genetic variability of germplasm using enzymatic markers. In: Colloque Explotation-Physiologie et Amelioration de L'Hevea. Montpellier, 1984. Compte Rendu. Montpellier, ICRA/GERDAT. p. 365—376 (1984). —— Hamrick, J. L.: Isozymes and analysis of genetic structure in plants populations. In: Soltis, D. E. and Soltis, P. S. (ed.): Isozymes in plant biology. Portland, Dioscorides Press. pp. 87—105 (1989). —— Institute de Recherches sur le Caoutchouc: Laboratoire d'électrophorèse. In: Rapport Annuel: 1985. Paris, IRCA. p. 33—35 (1986). —— Lebrun, P. and Chevallier, M. H.: Starch and polyacrylamide gel electrophoresis of *Hevea brasiliensis:* a laboratory manual. Montpellier, IRCA/CIRAD. 44p. (1988). —— Nei, M.: Genetic distance between population. Am. Nat. **106**: 283—292 (1972). —— Nei, M.: Analysis of gene diversity in subdivided populations. Proc. Natl. Acad. Sci. **70**: 3321—3323 (1973). —— Nei, M.: F-statistics and analyses of gene diversity in subdivided populatons. Ann. Human Genet. **41**: 225—233 (1977). —— Swofford, D. L.: Biosys-1: User's Manual. Illinois. 43p. (1989). —— Wright, S.: The interpretation of population structure by F-statistics with special regard to systems of mating. Evolution **19**: 395—420 (1965). —— Wright, S.: Evolution and genetics of populations. Vol. 4. Variability within and among natural populations. University of Chicago Press, Chicago (1978). —— Wycherley, P. R.: The genus *Hevea*. In: Worksshop in International Collaboration Hevea Breeding and the Collection an Establishment of Materials from the Neotrophic. 1977. Kuala Lumpur. 12 p. (1977).

Modulo Tile Constructions for Systematic Seed Orchard Designs

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Summary

Seed orchard designs purport to maximize outcrossing by having each clone as a near neighbour of every other clone, and to miniminze inbreeding by maintaining maximum separation between ramets of the same clone. This paper initially presents quantitative descriptors that measure how well a design achieves these aims. Modulo tile designs are subsequently introduced. These designs are new generalizations of the conventional systematic designs, but have superior performance with regard to the design descriptors. Modulo tile designs have well-defined properties and are applicable to any sufficiently large number of clones. Also incorporated are 2 examples of how clone numbering may be altered on the basis of known flowering phenology in order to achieve special effects with the modulo tile designs.

Key words: seed orchard designs, systematic designs, monoecious species, panmixia, inbreeding depression.

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Introduction

The physical arrangement of clones in seed orchards is designed to minimize inbreeding and maximize outcrossing. For monoecious species, these aims may be achieved by ensuring that ramets of any particular clone are well separated by other clones, and by surrounding each clone with as many genetically diverse neighbours as possible.

It is not a trivial matter to generate a seed orchard design which possesses these desirable properties. Computer programs which may use sophisticated search techniques are sometimes deployed, e.g. La Bastide (1967), Bell and Fletcher (1978), Marsh (1985), Vanclay (1986, 1991), Chakravarty and Bagchi (1993). Sometimes standard statistical designs have been adapted by controlling planting positions within blocks, in particular the balanced incomplete block designs of Dyson and Freeman (1968), and Freeman (1967, 1969). Langner (1953) suggested the use of systematic designs and the properties of these designs were extensively investigated by Giertych (1965, 1971). Miscellaneous other designs such as the shifting-clone design of Malac (1962) have also been proposed. Giertych (1975) provides a good review of known seed orchard design constructions.

This paper introduces some quantitative descriptors which a plant breeder can use to evaluate and compare alternative seed orchard designs. It then proceeds to expound on modulo tile constructions, which are a generalization of conventional systematic designs. In these new constructions each ramet of a particular clone may be surrounded by one of several different sets of near neighbours. Thus it is possible to surround a clone with up to 36 different neighbouring clones, whereas in the usual systematic designs each clone can be surrounded by only 8 different clones.

A plant breeder who wishes to implement one of these modulo tile constructions and who has no desire to follow the theoretical development need only refer to the 2 sections marked with asterisks.

Assumptions used in constructing seed orchard designs

Table 1 depicts a small seed orchard design with 25 clones in a square planting arrangement. Clone number 1 at position row 4, column 4 has clones 2, 3, 4, 5 as nearest neighbours and clones 6, 7, 8, 9 as diagonal neighbours. In this paper the nearest and diagonal neighbours of any plant position are collectively called the first order square neighbourhood, or more briefly, the first neighbourhood. By collecting arrangements of plants in ever increasing squares about a subject plant, it is possible to obtain second order square neighbourhoods, third order square neighbourhoods, and so on. *Table 1* displays the complete first, second and third neighbourhoods of a subject plant.

Table 1. — Section of a seed orchard in a square arrangement. The heavy shading is the first order square neighbourhood of clone number 1, and the light shading is the second order square neighbourhood.

7	2	3	4	5	14	6
9	10	11	12	13	14	18
5	15				16	7
20	17		1		18	14
18	19				20	8
17	21	22	23	24	25	9
16	15	14	13	12	11	10

If wind direction is quite variable, it is expected that the nearest neighbours of any plant will be the major sources of pollen. However, even under conditions of complete canopy closure or near canopy closure, the diagonal neighbours may provide considerable amounts of pollen. With regard to outcrossing, the following assumptions will be made.

(1) All plants in the first neighbourhood of a subject plant are pollinators of the subject plant.

(2) No other plants are pollinators of the subject plant.

(3) All plants in the first neighbourhood are equally effective as pollinators. In particular, no distinction is made between nearest neighbours and diagonal neighbours even though the latter are at a greater distance from the subject plant.

In seed orchard design literature, many authors have implicitly or explicitly adopted these assumptions, e.g. Langner and Stern (1955), Malac (1962), Freeman (1969), Vanclay (1991). Genetic marker studies have also indicated that the pollinators of an individual tend to be its near neighbours, e.g. Shen et al. (1981), Erickson and Adams (1989). Although the reasonableness of the above assumptions may be a matter of considerable conjecture, e.g. Adams and Birkes (1990), they do lead to useful methods of describing and comparing seed orchard designs.

Quantitative measures of outcrossing potential in seed orchard designs

Throughout this paper, the border trees of any orchard layout are assumed to provide a buffer between the interior trees and possible external sources of pollen. Therefore in any calculations, the border trees are assumed to be pollinators, but are not regarded as subject trees for seed collecting purposes.

Pollinator matrix

The pollinator matrix P is defined to have elements P_{ij} = number of times that clone j is in a first neighbourhood of clone i.

Table 2. — Pollinator matrix for the design in *table 1.*

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
1	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	1	0	1	1	0	1	1	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
3	1	1	0	0	1	1	0	1	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0
4	1	1	0	0	1	0	1	0	1	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0
5	1	0	1	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0
6	1	1	1	0	0	0	0	0	0	1	1	1	0	0	1	0	1	0	0	0	0	0	0	0	0
7	1	1	0	1	0	0	0	0	0	0	0	1	1	1	0	1	0	1	0	0	0	0	0	0	0
8	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	1	1	0	0
9	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	1	1
10	0	1	1	0	1	1	1	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
11	0	2	1	1	0	1	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
12	0	1	1	1	1	1	1	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
13	0	1	0	1	1	0	1	0	0	0	0	1	0	2	0	1	0	0	0	0	0	0	0	0	0
14	0	0	0	0	1	1	2	0	0	0	0	0	1	1	0	1	0	1	0	0	0	0	0	0	0
15	0	0	1	0	1	1	0	0	1	1	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0
16	0	0	0	1	0	0	2	0	0	0	0	0	1	2	0	0	0	2	0	0	0	0	0	0	0
17	0	0	1	0	1	1	0	1	0	0	0	0	0	0	1	0	0	1	1	1	0	0	0	0	0
18	0	0	0	1	0	0	2	1	1	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0
19	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	2	1	0	1	1	1	0	0	0
20	0	0	0	1	0	0	0	1	2	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	1
21	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	1	1	1	0	0	1	0	0	0
22	0	0	0	0	1	0	0	1	0	0	0	0	1	1	1	0	0	0	1	0	1	0	1	0	0
23	0	0	0	0	1	0	0	1	1	0	0	1	1	1	0	0	0	0	0	0	0	1	0	1	0
24	0	0	0	0	1	0	0	0	1	0	1	1	1	0	0	0	0	0	0	1	0	0	1	0	1
25	0	0	0	0	0	0	0	1	2	1	1	1	0	0	0	0	0	0	0	1	0	0	0	1	0

Thus the pollinator matrix summarizes the outcrossing combinations of a seed orchard design, subject to the above assumptions. For example, in the pollinator matrix of *table 2*,
$P_{1,2} = P_{1,3} = P_{1,4} = P_{1,5} = P_{1,6} = P_{1,7} = P_{1,8} = P_{1,9} = 1$, and all other elements of the first row are 0. This is because there is only one plant of clone 1 in *table 1* and its first neighbourhood consists of one ramet of each of clones 2 to 9.

Langner and Stern (1955) present the elements of the upper right triangle of several pollinator matrices and so these authors are using the concept of a pollinator matrix without actually defining it. Although the pollinator matrix is a complete representation of the outcrossing possibilities in a seed orchard, it can be large and unwieldy. It is therefore convenient to define 2 numeric parameters which summarize the outcrossing potential of a seed orchard design.

Percent adjacency

The percent adjacency, %Adj, for clone i is defined to be the percentage of all other clones which are a near neighbour of clone i at least once. The percent adjacency for a whole orchard design is defined to be the mean of the percent adjacencies for all clones in the design.

Percent adjacency measures the success of the design in allowing any clone to receive pollen from every other clone, but it does not take into account the proportions of pollen received from the other clones. It is very easy to calculate. For example, in *table 2*

%Adj for clone 1 = 8/24 · 100 % = 33.3 %
%Adj for clone 13 = 7/24 · 100 % = 29.2 %, and
%Adj for whole design = (8 + 8 + 8 + ... + 7)/25/24 · 100 %
= 190/25/24 ·100 % = 31.7 %

Percent outcrossing uniformity

For arbitrary clone i, let $f_1, f_2, ..., f_{i-1}, f_{i+1}, ... f_n$ be the frequencies for which each of the other clones are a near neighbour of clone i. These frequencies may be obtained from the i^{th} row of the pollinator matrix. Let SD_i denote the standard deviation of these frequencies. Then the percent outcrossing uniformity, %OU, for clone i is defined to be $100/(1 + SD_i)$%. The percent outcrossing uniformity for the whole design is defined to be the mean percent outcrossing uniformity of all clones in the design.

For example, with regard to clone 1 in the pollinator matrix of *table 2*, the neighbour frequencies are 1,1,1,1,1,1, 1,1,0,0,...,0. The sum is 8, the uncorrected sum of squares is also 8, the corrected sum of squares is $8 - 8^2/24 = 5.333$, the variance is
5.333/24 = 0.222, the standard deviation is 0.471, and the %OU is 68.0 %. The %OU for the whole design is
(68.0 % + 68.0 % + ... + 64.4 %)/25 = 66.6 %.

For both %Adj and %OU a low percentage is indicative of relatively poor outcrossing and a high percentage indicates good outcrossing potential. It should be emphasized that for certain numbers of plants and/or clones, 100 %Adj and/or 100 %OU are theoretically unachievable. This does not prevent these parameters from being useful descriptors for comparing designs of a fixed size for a fixed number of clones.

Quantitative measures of inbreeding potential in seed orchard designs

Inbreeding avoidance rating

The inbreeding avoidance rating, IAR, for clone i is the smallest order square neighbourhood of clone i which contains another ramet of clone i. For example, since ramets of clone 14 are nearest neighbours in column 6 of *table* 1, clone 14 has an inbreeding avoidance rating of 1. Looking along row 3 reveals that clone 7 has an inbreeding avoidance rating of 2. Inspection of column 3 reveals that clone 3 has an inbreeding avoidance rating of 3. Clone 1 is said to have an infinite inbreeding avoidance rating since there is only one ramet of the clone.

The inbreeding avoidance rating of a whole design is defined to be the minimum IAR of all clones in the design. Thus the design in *table 1* has an IAR of 1. In all cases, the higher the IAR the better.

Percent inbreeding intolerance

In the introduction, it was assumed that only plants in the first neighbourhood of a subject tree would be pollinators of that tree. If it is necessary to be very careful to avoid inbreeding depression, then it might be undesirable to collect seeds from any tree which had another ramet of the same clone in the first or second neighbourhood. The percent inbreeding intolerance, %II, is the percentage of plants in the design from which seed would be collected. Obviously, the inbreeding intolerance is 100% if and only if the IAR of a design is at least 3.

For example, in *table 1*, if the intention is to minimize inbreeding depression then the interior plants at positions (2,6), (3,4), (3,5), (4,2), (4,6), and (5,5) would be rejected. Since there are 25 trees in the interior of the design, the %II is (25-6)/25 · 100% = 76%.

Modulo tile designs

*** *Modulo addition* ***

Modulo arithmetic is a simple number theoretic concept which basically deals with remainders after division, and an understanding of modulo addition is required for the construction of modulo tile designs.

Suppose there are just five clones in a design and they are numbered 1 to 5 inclusive, then 5 is called the modulus and this simply means that no number can be greater than 5. Thus to count 10 items 1 would normally say 1,2,3,4,5,6,7, 8,9,10; but to count the same items modulo 5 one would say 1,2,3,4,5,1,2,3,4,5. In modulo 5 arithmetic, any number, such as 10, which is a multiple of 5 is converted to 5, and any other number is converted to the remainder after division by 5. For example, 6=5x1+1 and so 6 is converted to 1 and we say that 6 equals 1 modulo 5, or 6 = 1 (mod 5). Similarly, 13=5x2+3 and we say 13 equals 3 modulo 5.

Modulo addition works in a similar fashion — just add 2 numbers in the usual way and then convert the answer using the modulus. For example, 3+4=7 and since 7=5x1+2 we have 3+4 equals 2 modulo 5.

Derivation of modulo tile concepts from other designs

Table 3 presents a systematic design for 10 clones and is derived from Langner (1953). As well as special constructions for certain numbers of clones, Giertych (1965, 1971) performed a detailed investigation of these systematic designs with the special purpose of maximizing distances between ramets of the same clone. The main feature of these designs is that each row is effectively a cyclic permutation of the first row. In *table 3*, clone 1 is always immediately below clone 8, and using Giertych's nomenclature, clone 8 is called the indicator value for the design. An alternative perspective on this construction is to regard clone 1 as the initial value. Subsequent clones in any row

Table 3. — A Langner-Giertych systematic design for 10 clones.

1	2	3	4	5	6	7	8	9	10	1	2
4	5	6	7	8	9	10	1	2	3	4	5
7	8	9	10	1	2	3	4	5	6	7	8
10	1	2	3	4	5	6	7	8	9	10	1

Table 4. — Section of a Freeman nondirectional seed orchard design for 17 clones.

16	4	5	12	7	11	2	9	16	4	5	12
13	1	14	3	6	10	8	15	13	1	14	3
17	5	6	13	8	12	3	10	17	5	6	13
14	2	15	4	7	11	9	16	14	2	15	4
1	6	7	14	9	13	4	11	1	6	7	14
15	3	16	5	8	12	10	17	15	3	16	5

Table 5. — Section of a 2 x 2 tile design for 15 clones using row addend 5 and column addend 4.

7	8	12	13	2	3
9	10	14	15	4	5
11	12	1	2	6	7
13	14	3	4	8	9
15	1	5	6	10	11
2	3	7	8	12	13

Table 6. — Section of a 2 x 2 tile design for 15 clones using row addend 5 and column addend 4.

8	9	13	14	3	4
10	11	15	1	5	6
12	13	2	3	7	8
14	15	4	5	9	10
1	2	6	7	11	12
3	4	8	9	13	14

are obtained by adding 1 modulo 10 to the previous clone. Subsequent clones in any column are obtained by adding 3 modulo 10 to the previous clone. The Langner-Giertych designs are modulo tile designs where the tile consists of only 1 row and only 1 column.

Table 4 displays a section of a seed orchard design for 17 clones as described by Freeman (1969). Although Freeman did not use modulo tile techniques, the finished product is a tile design based on 2 rows by 8 columns. Subsequent tiles to the right have zero added modulo the number of clones, i.e. tiles within any row of tiles are all identical. Subsequent tiles in any column of tiles have 1 added modulo the number of clones.

Definition and properties of modulo tile designs

A tile consists of a rectangular array of clones. A modulo tile design is created by placing an initial tile at the top lefthand corner of a region. A new tile may be added to the right of any tile after first adding a constant modulo the total number of clones in the design. This constant is called the row addend. A new tile may be added below any tile after first adding a constant modulo the total number of clones. This constant is called the column addend.

Consider the 2x2 tile design in *table 5,* where the initial tile consists of 2 rows by 2 columns and holds clones 7, 8, 9 and 10. The pollinators of clone 1 at relative position row 1, column 1 of the central tile are 10, 14, 15, 12, 2, 14, 3, 4. These pollinators can be rewritten modulo 15 as 1—6, 1—2, 1—1, 1—4, 1+1, 1—2, 1+2, 1+3. The point to note is that these sums and differences modulo 15 will indicate the pollinators of any clone which happens to fall at relative position row 1, column 1 of any tile. For example, *table 6* is the same design as *table 5,* but with a different initial tile and with clone 2 falling at the relevant position of the central tile. The pollinators of this clone 2 are 2—6, 2—2, 2—1, 2—4, 2+1, 2—2, 2+2, aid 2+3, all modulo 15. The increments and decrements —6, —2, —1, —4, +1, —2, +2, +3 establish the neighbourhood profile, or pollinator profile, of any clone at the relevant position.

A little reflection shows that for any modulo tile design, all clones which fall at the same relative position within any tile will have equivalent neighbourhood profiles, i.e. the same increments and decrements for determining first neighbourhoods. In order for each clone to have maximum variety of pollinators it is therefore essential that the row and column addends be chosen to ensure that every clone occurs at every possible relative position within a tile. The following theory shows how this may be achieved.

Theorem: The equation $i + xR + yC \equiv m \pmod{n}$, where i, R, C, m and n are fixed, has integer solutions for x, y if and only if ((R,C),n) divides (m—i), where (s,t)) denotes the greatest common divisor of arbitrary integers s and t.

Proof: See the appendix.

Corollary: Every clone will occur at every relative position within a tile if the row and column addends are relatively prime, i. e. if the only whole number which divides both the row addend and the column addend is 1.

Proof: Suppose clone i is at some relative position of a tile. Let m be any other clone number. If the row addend, R, and column addend, C, are relatively prime then (R,C) = 1. Therefore ((R,C),n) = (1,n) = 1 so that ((R,C),n) divides (m—i). Now by invoking the theorem, shifting x tiles to the right (or left) and y tiles down (or up) will locate a tile which has clone m at the same relative position as clone i, and the result follows.

In special cases, other solutions are possible. For example, if n is odd then it is sufficient to choose R, C such that (R, C) = 2 or (R,C) = 1.

If one is searching for tile constructions which are effective for arbitrary numbers of clones, then one should only consider row and column addends which are relatively prime. Under these circumstances, each tile design will incorporate exactly n different tiles, and if each tile is r rows by c columns then each clone will have exactly rc different first neighbourhoods. Furthermore, all clones will tend to have the same clonal %Adj, the same clonal %OU, the same clonal IAR, and identical pollinator profiles. In practice, some of these parameters might vary a little from clone to clone because orchard shape and size might lead to slightly different clonal replications.

The search for optimum modulo tile designs

1x1 Tiles

The 1x1 tiles were fully investigated by GIERTYCH (1965, 1971). As modulo tile designs, they are not very interesting because each clone has only one possible first neighbourhood and therefore exactly 8 pollinators. If the row addend is 1 and the column addend is 3 then it is easy to verify that if the number of clones is at least 9 then the 1x1 modulo tile designs have 100 % II and pollinator profile —4, —3, —2, —1, 1, 2, 3, 4.

1x2 Tiles

If the initial tile is restricted to only clones 1 and 2 then it must be of the form (1 2) or (2 1). All possible relatively prime pairs of row and column addends between 1 and 7 inclusive were initially tested on 15 and 20 clones in order to find addends which yielded IAR's of at least 3 and high %Adj's and high %OU's. The better performing addends were subjected to detailed comparisons for all clone numbers between 10 and 40. It was found that the good performers all had comparable design parameters for 20 or more clones, and that they differed considerably for fewer than 20 clones. The best addends were R = 1, C = 5 for initial tile (2 1). The pollinator profile for this optimum 1x2 tile design is given in *table* 7 and involves 14 clones.

2x2 Tiles

All possible arrangements of clones 1, 2, 3, 4 in an initial 2x2 tile, and all possible pairs of relatively prime addends within the range 1 to 7 were screened for IAR $\geq$ 3, maximum %Adj and maximum %OU. The optimum 2x2 tile was $\begin{pmatrix} 4 & 3 \\ 2 & 1 \end{pmatrix}$ with row addend 4 and column addend 7. For large numbers of clones, arbitrary clone i has 20 pollinators with relative frequencies as per *table 8*.

3x3 Tiles

All possible arrangements of clones 1 to 9 in an initial 3x3 tile, and all possible pairs of relatively prime addends within the range 1 to 11 were screened for IAR $\geq$ 3, maximum %Adj and maximum %OU. A compromise was reached between maximizing these desirable design parameters and finding a design which was effective for relatively small numbers of clones. The eventual chosen initial tile was $\begin{pmatrix} 8 & 9 & 4 \\ 7 & 1 & 2 \\ 6 & 3 & 5 \end{pmatrix}$ with R = 5 and C = 11. For large numbers of clones, arbitrary clone i has 36 pollinators with relative frequencies as per *table 9*.

Table 7. — Pollinator profile for the optimum 1 x 2 modulo tile design.

Pollinators of clone i	Relative frequency of pollinators
-7	1
-6	1
-5	2
-4	1
-3	1
-2	1
-1	1
1	1
2	1
3	1
4	1
5	2
6	1
7	1

*** Examples and use of the optimum modulo tile designs***

The choice of modulo tile design depends on the total number of clones, and on the number of different clones that the breeder requires to be adjacent to any particular clone. All of the designs in this section have an inbreeding avoidance rating of at least 3, which means that there is adequate separation between ramets of the same clone.

Table 3 is an example of a conventional systematic design in which each ramet of a particular clone has the same 8 near neighbours. For example clone 5 always has clones 1, 2, 3, 4, 6, 7, 8, 9 as neighbours. This can be seen by considering the ramets of clone 5 in the second and third rows. Similarly, clone 6 always has clones 2, 3, 4, 5, 7, 8, 9, 10 as neighbours. These conventional designs are 1x1 tile designs and can be used whenever there are at least 9 clones and whenever the breeder is content for each clone to have exactly 8 different neighbours. These designs may be constructed by placing a 1 at the top left-hand corner and, by using addition modulo the number of clones, continue to add 1 to the previous clone number in the same row, and add 3 to the previous clone number

Table 8. — Pollinator profile for the optimum 2 x 2 modulo tile design.

Pollinators of clone i	Relative frequency of pollinators
-14	1
-10	1
-9	2
-8	1
-7	1
-5	2
-4	1
-3	2
-2	2
-1	3
1	3
2	2
3	2
4	1
5	2
7	1
8	1
9	2
10	1
14	1

Table 9. — Pollinator profile for the optimum 3 x 3 modulo tile design.

Pollinators of clone i	Relative frequency of pollinators	Pollinators of clone i	Relative frequency of pollinators
-19	1	1	5
-17	1	2	4
-16	1	3	3
-15	1	4	3
-14	1	5	2
-13	1	6	2
-12	1	7	3
-11	1	8	2
-10	2	9	2
-9	2	10	2
-8	2	11	1
-7	3	12	1
-6	2	13	1
-5	2	14	1
-4	3	15	1
-3	3	16	1
-2	4	17	1
-1	5	19	1

in the same column. Alternatively, the breeder may use the indicator values of GIERTYCH (1965, 1971) in order to maximize distances between ramets of the same clone.

If the breeder has at least 13 clones and requires that each clone has up to 14 different near neighbours then the 1x2 tile design may be used. The first 2 clone numbers are (2 1) and this tile should be placed at the top lefthand corner. The row addend is 1 and the column addend is 5. This means that the next tile along each row has 1 added to each clone in the previous tile, with all addition being carried out modulo the number of clones. Thus the second tile in the first row is (3 2), the third tile (4 3), and so on. The next tile down any column of tiles has 5 added to each clone in the previous tile. Thus the second tile in the first column of tiles is (7 6). *Table 15a* is an example of a 1x2 tile design.

If the breeder has at least 15 clones and requires that each clone has up to 20 different near neighbours then the 2x2 tile design may be used. The tile $\begin{pmatrix}4 & 3\\ 2 & 1\end{pmatrix}$ should be placed in the top lefthand corner, and the addends 4, 7 should be used. Thus the next tile along each row has 4 added to each clone in the previous tile, with all addition being carried out modulo the number of clones. Consequently the second tile in the first row is $\begin{pmatrix}8 & 7\\ 6 & 5\end{pmatrix}$. The next tile down any column of tiles has 7 added to each clone in the previous tile. Thus the second tile in the first column of tiles is $\begin{pmatrix}11 & 10\\ 9 & 8\end{pmatrix}$. Proceeding in this manner, the 4 tiles in the top lefthand corner will generate the following section of a seed orchard design.

$$\begin{bmatrix}4 & 3 & 8 & 7\\ 2 & 1 & 6 & 5\\ 11 & 10 & 15 & 14\\ 9 & 8 & 13 & 12\end{bmatrix}$$

If the breeder has at least 24 clones and requires that each clone has up to 36 different near neighbours then the 3x3 tile design may be used. The tile $\begin{pmatrix}8 & 9 & 4\\ 7 & 1 & 2\\ 6 & 3 & 5\end{pmatrix}$ should be placed in the top lefthand corner, and the addends 5, 11 should be used. Thus the next tile along each row has 5 added to each clone in the previous tile, with all addition being carried out modulo the number of clones. The second tile in the first row is therefore $\begin{pmatrix}13 & 14 & 9\\ 12 & 6 & 7\\ 11 & 8 & 10\end{pmatrix}$. The next tile down any column of tiles has 11 added to each clone in the previous tile. Thus the second tile in the first column of tiles is $\begin{pmatrix}19 & 20 & 15\\ 18 & 12 & 13\\ 17 & 14 & 16\end{pmatrix}$. Proceeding in this manner, the 4 tiles in the top lefthand corner will generate the following section of a seed orchard design.

$$\begin{bmatrix}8 & 9 & 4 & 13 & 14 & 9\\ 7 & 1 & 2 & 12 & 6 & 7\\ 6 & 3 & 5 & 11 & 8 & 10\\ 19 & 20 & 15 & 24 & 25 & 20\\ 18 & 12 & 13 & 23 & 17 & 18\\ 17 & 14 & 16 & 22 & 19 & 21\end{bmatrix}$$

Table 10. — Do the designs have minimum IAR ≥ 3? (y=yes, n=no, n/a=design not available).

Number of clones	Langner-Giertych	Optimum 1x2 Tile	Optimum 2x2 Tile	Optimum 3x3 Tile	Freeman
10	n	n	n	n	n/a
11	y	n	n	n	n/a
12	y	n	n	n	n/a
13	y	y	n	n	n/a
14	y	y	n	n	n/a
15	y	y	y	n	n/a
16	y	y	y	n	n/a
17	y	y	y	n	n
18	y	y	y	n	n
19	y	y	y	n	n
20	y	y	y	n	n
21	y	y	y	n	n
22	y	y	y	n	n
23	y	y	y	n	n/a
24	y	y	y	y	n
25	y	y	y	y	n
26	y	y	y	y	n/a
27	y	y	y	y	n/a
28	y	y	y	y	n
29	y	y	y	y	n
30	y	y	y	y	n/a
31	y	y	y	y	n
32	y	y	y	y	n
33	y	y	y	y	n
34	y	y	y	y	n
35	y	y	y	y	n/a
36	y	y	y	y	n/a
37	y	y	y	y	n/a
38	y	y	y	y	n/a
39	y	y	y	y	n/a
40	y	y	y	y	n/a

Table 11. — Percent adjacencis for various designs. For n clones, the layout is (n+2) rows by (n+2) columns.

Number of clones	Langner-Giertych	Optimum 1x2 Tile	Optimum 2x2 Tile	Optimum 3x3 Tile
10				
11	80			
12	73			
13	67	100		
14	62	100		
15	57	100	100	
16	53	93	100	
17	50	88	88	
18	47	82	88	
19	44	78	89	
20	42	74	100	
21	40	70	90	
22	38	67	86	
23	36	64	82	
24	35	61	78	100
25	33	58	83	100
26	32	56	80	100
27	31	54	77	100
28	30	52	70	100
29	29	50	71	100
30	28	48	69	100
31	27	47	67	100
32	26	45	65	100
33	25	44	63	100
34	24	42	61	100
35	24	41	59	100
36	23	40	57	97
37	22	39	56	100
38	22	38	54	95
39	21	37	53	95
40	21	36	51	92

Table 12. — Percent outcrossing uniformities for various designs. For n clones, the layout is (n±2) rows by (n+2) columns.

Number of clones	Langner-Giertych	Optimum 1x2 Tile	Optimum 2x2 Tile	Optimum 3x3 Tile
10				
11	18.5			
12	15.8			
13	14.0	24.4		
14	12.8	25.3		
15	11.9	25.1	23.1	
16	11.1	22.0	23.7	
17	10.5	19.0	18.7	
18	10.0	17.1	18.7	
19	9.6	15.6	16.7	
20	9.2	14.6	22.9	
21	8.9	13.7	18.2	
22	8.6	13.0	17.6	
23	8.3	12.3	14.9	
24	8.0	11.8	15.3	29.2
25	7.8	11.4	15.6	26.9
26	7.6	11.0	15.0	26.1
27	7.4	10.6	14.2	22.1
28	7.3	10.3	13.1	25.4
29	7.1	10.0	13.1	23.2
30	6.9	9.7	12.6	22.9
31	6.8	9.4	12.2	20.6
32	6.7	9.2	11.8	19.9
33	6.5	9.0	11.5	19.8
34	6.4	8.8	11.1	18.6
35	6.3	8.6	10.8	17.9
36	6.2	8.4	10.6	17.1
37	6.1	8.3	10.3	17.0
38	6.0	8.1	10.1	16.2
39	5.9	8.0	9.9	15.6
40	5.8	7.8	9.7	15.0

Table 13. — Are various designs thinnable? (y=yes, n=no).

Number of clones	Langner-Giertych	Optimum 1x2 Tile	Optimum 2x2 Tile	Optimum 3x3 Tile
10				
11	y			
12	n			
13	y	y		
14	n	y		
15	y	y	n	
16	n	y	y	
17	y	y	y	
18	n	n	n	
19	y	n	y	
20	n	n	y	
21	y	n	y	
22	n	n	n	
23	y	y	y	
24	n	y	y	n
25	y	y	y	n
26	n	y	y	n
27	y	y	y	n
28	n	y	y	n
29	y	y	y	n
30	n	y	y	n
31	y	y	y	n
32	n	y	y	n
33	y	y	y	n
34	n	y	y	n
35	y	y	y	n
36	n	y	y	n
37	y	y	y	n
38	n	y	y	n
39	y	y	y	n
40	n	y	y	n

It is a straightforward matter to write computer programs which will generate modulo tile designs for an arbitrary number of clones and arbitrary orchard size.

Discussion

Tables 10, 11, 12 and *13* summarize the properties of some modulo tile designs for small numbers of clones. If inbreeding avoidance is essential, then a minimum standard for any seed orchard design is that the IAR should be at least 3. Thus *tables 11, 12* and *13* only provide data for numbers of clones for which this standard is achieved. In *table 13,* a design is said to be thinnable if a mechanical thinning of every second row, and every second tree in the remaining rows, leaves a design which still has the full complement of clones and which still has a minimum IAR of 3. It should be noted that the Langner-Giertych designs in *tables 10* to *13* invoke the indicator values in Giertych (1965), rather than the fixed addends 1,3.

The Freeman designs actually have excellent %OU's of approximately 40 % to 50 %, but their %II's range from 26 % to 86 %, with most being below 60 %. The prospect of rejecting a comparatively large proportion of the trees in an orchard on the basis of possible inbreeding depression means that the Freeman designs need no further consideration in this paper.

With regard to numbers of pollinators, *table 11* shows that even the simplest nontrivial modulo tile designs, 1x2, offer a considerable improvement over Langner-Giertych designs. As a general rule, *tables 11* and *12* show that as tile size increases, better design parameters are achievable,

Table 14. — Methods of relabeling 40 clones according to flowering phenology in order to maximize panmixia or seed production. The new clone numbers are phenological ranks with number 1 being earliest flowering and number 40 latest flowering.

Original clone number	New clone number for maximizing panmixia	New clone number for maximizing seed production	Original clone number	New clone number for maximizing panmixia	New clone number for maximizing seed production
1	1	18	21	23	23
2	6	16	22	28	25
3	11	14	23	33	27
4	16	12	24	38	29
5	21	10	25	4	31
6	26	8	26	9	33
7	31	6	27	14	35
8	36	4	28	19	37
9	2	2	29	24	39
10	7	1	30	29	40
11	12	3	31	34	38
12	17	5	32	39	36
13	22	7	33	5	34
14	27	9	34	10	32
15	32	11	35	15	30
16	37	13	36	20	28
17	3	15	37	25	26
18	8	17	38	30	24
19	13	19	39	35	22
20	18	20	40	40	21

but at the expense of applicability to small numbers of clones.

Within any tile size, the clonal arrangement within the initial tile and the values of the row and column addends have a considerable impact on the design properties. As tile size increases, it is essential to use a computer to search through the various possibilities. Eventually a compromise must be reached between maximizing %Adj and %OU, and choosing a design which will also be adequate for comparatively small numbers of clones. However, once a design is chosen for a given tile size, it can be used for arbitrarily large numbers of clones and the profile of pollinators of any clone will be known exactly, as in *tables 7, 8* and *9*.

Table 15a. — Section of an optimum 1x2 design for 40 clones.

2	1	3	2	4	3	5	4	6	5	7	6	8	7	9	8	10	9	11	10
7	6	8	7	9	8	10	9	11	10	12	11	13	12	14	13	15	14	16	15
12	11	13	12	14	13	15	14	16	15	17	16	18	17	19	18	20	19	21	20
17	16	18	17	19	18	20	19	21	20	22	21	23	22	24	23	25	24	26	25
22	21	23	22	24	23	25	24	26	25	27	26	28	27	29	28	30	29	31	30
27	26	28	27	29	28	30	29	31	30	32	31	33	32	34	33	35	34	36	35
32	31	33	32	34	33	35	34	36	35	37	36	38	37	39	38	40	39	1	40
37	36	38	37	39	38	40	39	1	40	2	1	3	2	4	3	5	4	6	5

Table 15b. — Optimum 1x2 design with clones renumbered according to flowering phenology in order to maximize panmixia.

6	1	11	6	16	11	21	16	26	21	31	26	36	31	2	36	7	2	12	7
31	26	36	31	2	36	7	2	12	7	17	12	22	17	27	22	32	27	37	32
17	12	22	17	27	22	32	27	37	32	3	37	8	3	13	8	18	13	23	18
3	37	8	3	13	8	18	13	23	18	28	23	33	28	38	33	4	38	9	4
28	23	33	28	38	33	4	38	9	4	14	9	19	14	24	19	29	24	34	29
14	9	19	14	24	19	29	24	34	29	39	34	5	39	10	5	15	10	20	15
39	34	5	39	10	5	15	10	20	15	25	20	30	25	35	30	40	35	1	40
25	20	30	25	35	30	40	35	1	40	6	1	11	6	16	11	21	16	26	21

Table 15c. — Optimum 1 x 2 design with clones renumbered according to flowering phenology in order to maximize seed production.

16	18	14	16	12	14	10	12	8	10	6	8	4	6	2	4	1	2	3	1
6	8	4	6	2	4	1	2	3	1	5	3	7	5	9	7	11	9	13	11
5	3	7	5	9	7	11	9	13	11	15	13	17	15	19	17	20	19	23	20
15	13	17	15	19	17	20	19	23	20	25	23	27	25	29	27	31	29	33	31
25	23	27	25	29	27	31	29	33	31	35	33	37	35	39	37	40	39	38	40
35	33	37	35	39	37	40	39	38	40	36	38	34	36	32	34	30	32	28	30
36	38	34	36	32	34	30	32	28	30	26	28	24	26	22	24	21	22	18	21
26	28	24	26	22	24	21	22	18	21	16	18	14	16	12	14	10	12	8	10

In all of the searches only small row and column addends were tested, and only clones 1 to t, where t is the number of plant positions in a tile, were used in the initial tile. It seems plausible that use of larger addends and other clones in the initial tile will lead to designs with even greater %Adj's and %OU's, but which will fail for comparatively small numbers of clones.

Like the LANGNER-GIERTYCH designs, the modulo tile designs are easily adapted to any orchard shape. GIERTYCH (1965) placed considerable emphasis on mechanical thinning. It is clear from *table 13* that the 1x2 and 2x2 designs are more readily thinned than his designs, but the 3x3 tile is useless in this regard.

For 13 to 37 clones it is possible to achieve 100 % or close to 100 %Adj using one of the given modulo tile designs. For larger numbers of clones, the 3x3 tile design theoretically gives each clone 36 different pollinators and this is surely sufficient to guarantee adequate panmixia. On the other hand, the known pollinator identities and relative frequencies of the modulo tile designs can be used to take advantage of known flowering phenology. For example, WHEELER et al. (1993) state that phenologically synchronous clones may be separated if panmixia is a major aim; or they may be grown in close association in order to maximize seed production and reduce contamination from external pollen sources. Thus if forty clones are ranked according to flowering time, earliest to latest, then the allocation of clones to clone numbers according to *table 14* will help achieve the desired results if, for instance, the optimum 1x2 tile is chosen. *Table 15* depicts sections of the resulting seed orchard designs and *table 16* lists the pollinators of some key clones.

All of the design parameters such as %Adj and %OU are easily extended to hexagonal and triangular layouts. If a square design is "wobbled" by indenting every second row, and if the interrow spacing is appropriately adjusted, then a hexagonal layout is obtained (*Table 17*).

Table 16. — Pollinators of some key clones in *tables 15b* and *15c*.

Phenological clone 1 (earliest flowering)		Phenological clone 20 (mid flowering)		Phenological clone 40 (latest flowering)	
Pollinators for panmixia (Table 15b)	Pollinators for seed production (Table 15c)	Pollinators for panmixia (Table 15b)	Pollinators for seed production (Table 15c)	Pollinators for panmixia (Table 15b)	Pollinators for seed production (Table 15c)
6	2	1	7	1	26
10	3	5	9	5	27
11	4	6	11	6	28
15	5	10	13	10	29
16	6	11	15	11	30
20	7	15	17	15	31
21	8	24	19	16	32
25	9	25	23	20	33
26	10	29	25	21	34
30	11	30	27	25	35
31	12	34	29	26	36
35	13	35	31	30	37
36	14	39	33	31	38
40	15	40	35	35	39

It is clear that if a square design is wobbled then all of the first order neighbours of a subject plant in the ensuing hexagonal design are a subset of the first order square neighbours of the corresponding plant in the original square design. Also, the second order square neighbours of the hexagonal design are either first or second order neighbours of the square design. Thus if the square design has IAR $>$ 2 then so does the corresponding hexagonal design. Obviously, optimum square designs, such as the modulo tile designs in this paper, will lead to good hexagonal designs. However if optimum hexagonal designs are required then they should be subjected to direct investigation.

Table 17. — The 2 possible methods of wobbling the square design in *table 1* in order to obtain a hexagonal design.

7		2		3		4		5		14		6	
	9		10		11		12		13		14		18
5		15		6		2		7		16		7	
	20		17		3		1		4		18		14
18		19		8		5		9		20		8	
	17		21		22		23		24		25		9
16		15		14		13		12		11		10	

	7		2		3		4		5		14		6
9		10		11		12		13		14		18	
	5		15		6		2		7		16		7
20		17		3		1		4		18		14	
	18		19		8		5		9		20		8
17		21		22		23		24		25		9	
	16		15		14		13		12		11		10

Conclusions

Modulo tile constructions are powerful generalizations of the Langner-Giertych systematic designs. If a tile has been optimized then it is ready to be used for all sufficiently large numbers of clones. The known pollinator profiles of modulo tile designs may assist in achieving certain goals, such as those based on flowering phenology.

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References

Adams, W. T. and Birkes, D. S.: Mating patterns in seed orchards. Proc. 20th South. Forest Tree Improvement Conf., Charleston, South Carolina, June 27 to 29, 1989. 75—86 (1990). —— Bell, G. D. and Fletcher, A. M.: Computer organised orchard layouts (COOL) based on the permutated neighbourhood design concept. Silvae Genetica 27: 223—225 (1978). —— Chakravarty, G. N. and Bagchi, S. K.: A computer program for permutated neighbourhood seed orchard design. Silvae Genetica 41: 1—5 (1993). —— Dyson, W. G. and Freeman, G. H.: Seed orchard designs for sites with a constant prevailing wind. Silvae Genetica 17: 12—15 (1968). —— Erickson, V. J. and Adams, W. T.: Mating success in a coastal Douglas-fir seed orchard as affected by distance and floral phenology. Can. J. For. Res. 19: 1248—1255 (1989). —— Freeman, G. H.: The use of cyclic balanced incomplete block designs for directional seed orchards. Biometrics 23: 761—778 (1967). —— Freeman, G. H.: The use of cyclic balanced incomplete block designs for non-directional seed orchards. Biometrics 25: 561—571 (1969). —— Giertych, M.: M.: Systematic lay-outs for seed orchards. Silvae Genetica 14: 91—94 (1965). —— Giertych, M. M.: Systematic lay-outs for seed orchards. Silvae Genetica 20: 137—138 (1971). —— Giertych, M.: Seed orchard designs. In: Seed Orchards. (Ed. R. Faulkner). Forestry Commission Bulletin No. 54 (London): 25—37 (1975). —— La Bastide, J. G. A.: A computer program for the layouts of seed orchards. Euphytica 16: 321—323 (1967). —— Langner, W.: Die Klonanordnung in Samenplantagen. Z. Forstgenetik 2: 119—121 (1953). —— Langner, W. and Stern, K.: Versuchstechnische Probleme bei der Anlage von Klonplantagen. Z. Forstgenetik 4: 81—88 (1955). —— Malac, B. F.: Shifting-clone design for a superior tree seed orchard. Woodland Res. Notes, Union Bag-Camp Paper Corporation, Savannah, Georgia, U.S.A. 14: 1—3 (1962). —— Marsh, P. L.: A flexible computer algorithm for designing seed orchards. Silvae Genetica 34: 22—26 (1985). — Niven, I. and Zuckerman, H. S.: An Introduction to the Theory of Numbers. John Wiley & Sons Inc. (New York) (1972). —— Shen, H.-H., Rudin, D. and Lindgren, D.:

Study of the pollination pattern in a Scots pine seed orchard by means of isozyme analysis. Silvae Genetica **30**: 7—15 (1981). —— Vanclay, J. K.: Design for a gene recombination orchard. Silvae Genetica **35**: 1—3 (1986). —— Vanclay, J. K.: Seed orchard designs by computer. Silvae Genetica **40**: 89—91 (1991). —— Wheeler, N. C., Adams, W. T. and Hamrick, J. L.: Pollen distribution in wind-pollinated seed orchards. In: Advances in Pollen Management. Agriculture Handbook 698, Forest Service, United States Department of Agriculture: 25—31 (1993).

Appendix

Let (s,t) denote the greatest common divisor of arbitrary integers s and t, and let "|" denote the division without remainder property.

Theorem: The equation

$$i + xR + yC \equiv m \pmod{n} \qquad (1)$$

where i, R, C, m and n are fixed, has integer solutions for x, y if and only if ((R,C),n) | (m-i).

Proof. All equivalences will be modulo n, so the qualifier (mod n) will be omitted for convenience sake.

Case (a). Assume that R and C are relative prime, i.e. (R,C) = 1. From the Euclidean algorithm, e.g. Niven and Zuckerman (1972), there are integers x_0, y_0 such that

$$x_0R + y_0C = 1$$

$$\therefore\ x_0(m-i)R + y_0(m-i)C = m-i$$

$$\therefore\ i + x_0(m-i)R + y_0(m-i)C = m$$

$$\therefore\ i + xR + yC \equiv m$$

where $x \equiv x_0(m-i)$ and $y \equiv y_0(m-i)$.

Now note that ((R,C), n) = (1,n) = 1 which always divides (m-i).

Case (b). Assume ((R,C),n) = d where d > 1.

Necessity: If there is a solution to equation (1) then

$$i + xR + yC = m + kn \text{ for some } x, y, k.$$

$$\therefore\ xR + yC - kn = m-i.$$

Since d divides the lefthand side, it must also divide the righthand side, i.e. d | (m-i).

Sufficiency: Assume d | (m-i).

Since ((R/d,C/d),n/d) = 1, the Euclidean algorithm can be invoked and there must be x_0, y_0 such that

$$x_0(R/d,C/d) + y_0(n/d) = (m-i)/d.$$

There also exists x_1, y_1 such that

$$x_1(R/d) + y_1(C/d) = (R/d,C/d)$$

$$\therefore\ (m-i)/d - y_0(n/d) = x_0(R/d,C/d)$$

$$= x_0x_1(R/d) + x_0y_1(C/d)$$

Multiplying throughout by d gives

$$m - i - y_0n = x_0x_1R + x_0y_1C$$

$$\therefore\ x_0x_1R + x_0y_1C \equiv m - i$$

as required.

Genetic Variation in the Phenology of Flowering in Black Pine

By D. I. Matziris[1])

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Summary

The flowering phenology in black pine (*Pinus nigra* Arnold) was investigated in a clonal seed orchard for 2 successive years (1986 and 1987). The orchard was established in October 1978 in an area of 11 ha, at Koumani Peloponnesos, Greece and included 52 clones.

The results showed that significant genetic variation exists among clones in the commencement of the phenological stages of both, male and female flowers. Early and late flowering clones are not synchronized in receptivity and pollen shedding with the optimum time of the entire seed orchard and therefore the assumptions of panmictic equilibrium is violated. The date of commencement of flowering stages is under strong genetic control. The broad sense heritability values on individual tree basis were: 0.69 for the bud burst date in both years and 0.67 and 0.70 for the date of commencement of receptivity for the years 1986 and 1987, respectively. The H values on clone mean basis for the time of commencement of receptivity were 0.87 and 0.88 for the years 1986 and 1987, respectively.

The duration of flowering stages is under weak genetic control. The H values on individual tree basis of the duration of bud burst, were found 0.34 and 0.36 for the years 1986 and 1987 respectively. The corresponding H values for the duration of receptivity were 0.12 and 0.28. The date of commencement of pollen shedding is also weakly inherited characteristic (H=0.23), while the duration of pollen shedding is completely under environmental control. In all cases the year x clone interaction effect was insignificant indicating that the early flowering clones are maintained early in all years.

The duration of receptivity of individual flower was ranking from 2 days to 8 days, while the duration of the entire seed orchard was found 32 days and 27 days for the years 1986 and 1987 respectibely.

Key words: Black pine, seed orchard, genetic variation, genetic base, heritability, correlation, effective population size, flowering receptivity, panmixis.

FDC: 165.3; 165.53; 181.8; 181.521; 174.7 *Pinus nigra*; (495).

Zusammenfassung

In einer Klon-Samenplantage ist in den Jahren 1986 und 1987 die Blütenphänologie der Schwarzkiefer (*Pinus nigra*

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