

Minimum-Inbreeding Seed Orchard Design

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Abstract: The industrial concept of “quadratic assignment problem” (QAP) was used to develop a new seed orchard design that minimizes the level of inbreeding (minimum inbreeding [MI]) in an orchard’s seed crop through the optimum allocation of clones within the orchard’s grid. Spatial distribution of individual trees was done in proportion to their degree of genetic relatedness. The MI orchard design accommodates a variable number of unrelated or related clones with equal or variable sizes, and it is not restricted by the orchard’s spatial configuration (shape or size). The proposed design is suitable for advanced generation populations that commonly harbor complicated pedigree relationships. The MI design was compared with the commonly used permuted neighborhood design and the completely randomized scheme, resulting in aggregate inbreeding distances of 6.82, 12.53, and 22.56, respectively, highlighting the effectiveness of the proposed design. *FOR. SCI.* 56(6):603–608.

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SEED ORCHARDS REPRESENT THE LINK between tree breeding and operational forestry. They are the source of genetically improved seed used for the establishment of new forests. Before establishment of new orchards, several factors such as the number of selected genotypes (clones), number of copies (ramets) per clone, and the genetic relationship among selected genotypes should be considered to optimize their spatial distribution. An extensive array of seed orchard layouts such as pure rows, chessboard, completely random, randomized complete block, fixed block, rotating block, reversed block, unbalanced incomplete block, balanced incomplete block, cyclic incomplete block, balanced lattice, permuted neighborhood, and systematic designs have been proposed during the initial developmental phase of forest tree breeding programs during the 1950s to early 1970s (for a review, see Giertych 1975).

The permuted neighborhood design (COOL: Bell and Fletcher 1978, Chakravarty and Bagchi 1994) is considered to be the most efficient in randomizing the selected clones and separating their respective ramets through the use of a specified exclusion zone (i.e., number of positions between two ramets of the same clone) and hence was commonly used. However, it should be stated that the COOL design is only limited to situations in which clones are unrelated (i.e., the algorithm cannot separate related clones). In addition, although the exclusion zones in the COOL design are satisfied, resultant distances among genetic entities (ramets of the same clone) are not maximized (because of the local assignment); thus, the expected inbreeding rate in the orchard’s crop is not minimized. Inbreeding in the orchard’s crop leads to 1) losses of seed yield due to empty seed or low germination rate and 2) reduction of genetic gain in

forest plantations. As forest tree breeding advances, the unavoidable buildup of genetic similarities among the selected genotypes as well as the size of clonal representation (for proportional deployment concept, see Lindgren and Matheson 1986) creates additional constraints to reaching the optimum seed orchard design.

The complex nature of advanced generation orchards should accommodate the breeder’s desire to consider the selection of candidates from across generations consistent with the genetic evaluations performed over combined multigenerational data. Minimization of inbreeding with its different degrees of relationship, such as selfing (mating among ramets of the same clone and within trees), sib-mating (mating among individuals sharing a common parent), and parent-offspring (when forward and backward selections are made), becomes a key factor because relatedness inevitably accumulates with the completion of subsequent breeding cycles, and the impact of inbreeding on a the expression of a trait becomes a significant issue. These issues were recognized for advanced generation orchards; however, the proposed modifications were based on existing designs (e.g., Hodge and White 1993, El-Kassaby 2003, El-Kassaby et al. 2007).

The concept of the quadratic assignment problem (QAP) is frequently used to find the most “cost-efficient” allocation of facilities to equivalent number of locations, given the relationship (flow) among facilities and the distance among locations. Facilities with a high rate of interactions should be placed close to each other and vice versa to minimize the overall cost. Applications of QAP range from the allocation of electronic components into positions on a chip, design of factories, hospitals, distribution centers, image processing,

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or ranking of archaeological data. A detailed review of the QAP is provided by Loiola et al. (2007).

In this study, we propose an innovative minimum-inbreeding (MI) design to establish seed orchards while accounting optimally for variables such as relatedness with its various configurations, linear deployment, and when desired, positive assortative mating (fully relevant to advanced generations). Global assignment as presented here is adequately suited to simple situations (e.g., first-generation orchards) because it leads to the maximum separation among ramets of the same clone (i.e., minimizing the impact of inbreeding due to selfing). The MI design should be relevant to most commercially important forest tree species, but it may also be applicable in conservation programs of threatened species to ensure optimum deployment of a valuable reproductive material. Correspondingly, we present different orchard designs covering a wide array of possible deployment scenarios. Comparison with the commonly used COOL as well as the complete randomized design were made to evaluate the superiority of the MI design.

MI Seed Orchard Design

General Concept

There are n trees to be spatially distributed on an orchard's grid with n positions. Individual trees can be genetically related to each other with a magnitude expressed probabilistically from a pedigree. Possible genetic relationships among clones and their ramets may arise from selfing, mating among either full or half-sibs, and parent-offspring. The stronger the genetic relationship between two parental trees, the larger is the expected inbreeding coefficient in the orchard's seed crop (Falconer and Mackay 1996). Spatial distribution of trees on the orchard's grid substantially affects their mating pattern. Empirical studies suggest that the majority of pollen exchange occurs among close neighbors, and the chance of mating decreases with increased distance (e.g., Burczyk et al. 1996, 2002, Erickson and Adams 1989, Oddou-Muratorio et al. 2005).

Because of the detrimental effects of inbreeding on growth and other important traits (Orr-Ewing 1954, 1965), the objective of the proposed design is based on minimizing the overall inbreeding in the orchard's seed crop through spatial arrangement optimization (i.e., distance among related individuals), which can be restated as minimizing the planting of closely related trees within an elevated probability of gametic (pollen) exchange. However, this does not necessarily imply that mating among related trees does not occur (there are no predefined elimination rules or exclusion zones as those implemented in the COOL algorithm), but the resulting orchard layout (spatial allocation) is expected to lead to the minimum possible inbreeding in the orchard crop, given the particular information known before the orchard's establishment.

Mathematical Formulation

Let \mathbf{C} and \mathbf{D} be input matrices, both square, symmetric, with zeros on a diagonal, and of an order $n \times n$. The d_{ij} th

off-diagonal element of \mathbf{D} is the physical distance between the i th and the j th planting position on the orchard's grid. There are no assumptions on the distribution of the planting positions; usually, a square or rectangular arrangement is used. The c_{ij} th off-diagonal element of \mathbf{C} is calculated from a pairwise coancestry f_{ij} between trees i and j (f_{ij} is the probability that two alleles sampled randomly, one from individual i and the other from individual j , are identical copies of an ancestral allele (identity by descent, Malécot 1948) and suitably transformed, such as

$$c_{i,j} = 100(1 - f_{i,j}), \quad (1)$$

and rounded to the nearest integer value for computational simplicity. The constant (100) is then a desired precision factor. The inverse value reflects that lower genetic relationship is preferred over the lower distance.

Let ij be a pair of clones, where

$$i = 1, \dots, n; \quad j = 1, \dots, n; \quad i \neq j, \quad (2)$$

and let kl be a pair of positions, where

$$k = 1, \dots, n; \quad l = 1, \dots, n; \quad k \neq l, \quad (3)$$

The optimization problem can then be defined in terms of Boolean formulation (Koopmans and Beckmann 1957) as

$$\min \rightarrow \sum_{i,j=1}^n \sum_{k,l=1}^n c_{i,j} d_{k,l} x_{i,k} x_{j,l}, \quad (4)$$

subject to constraints (note that x are binary variables)

$$\sum_{i=1}^n x_{i,j} = 1 \quad \text{for } 1 \leq i \leq n, \quad (5)$$

$$\sum_{j=1}^n x_{i,j} = 1 \quad \text{for } 1 \leq j \leq n, \quad (6)$$

$$x_{i,j} \in \{0, 1\} \quad \text{for } 1 \leq i \wedge j \leq n. \quad (7)$$

Optimization

There are numerous optimization approaches to the QAP (Loiola et al. 2007). Because of the large problem sizes and the fact that QAPs are nondeterministic polynomial-time hard, we have selected a powerful modified tabu search algorithm specifically tailored to the QAPs (Misevicius 2005). We used a computer program developed and kindly provided to us by the same author (the program is based on the same algorithm). In general, the tabu search method is a deterministic neighborhood search with the ability to avoid entrapment in local optimums (Eiselt and Sandblom 2000). This method has been proven to be one of the most efficient heuristics for the QAP. It includes an iterated local search algorithm (denoted as intensification and diversification). Intensification is performed using a modified version of the robust tabu search algorithm, and diversification consists of application of special mutation operators to the locally optimum solutions. Solutions are improved by starting from carefully selected mutated local optima, rather than

assuming randomly scattered points. Details of the method are provided by Misevicius (2005).

Application

The method is demonstrated on a seed orchard block of 10 rows by 10 columns (100 planting positions) with a square planting grid using five alternative scenarios (Table 1). Under all scenarios, the task was to allocate 100 trees with their various genetic relationships to their respective planting positions using the MI design. A total of 20 clones, each with 5 ramets unless otherwise indicated, was used throughout the study. In the first scenario, clones were assumed to be unrelated. Therefore, the only nonzero off-diagonal elements in the relationship matrix are the ramets of the same clones (there were 5 ramets/clone). In the second scenario, 10 pairs of half-sibs were considered (clones 1 and 2, 3 and 4, ..., 19 and 20). In the third scenario, preferential pairing was investigated, in which ramets between the first 5 pairs of clones were preferentially allocated as neighbors (clones 1 and 2, 3 and 4, ..., 9 and 10) (note: these 5 clones as well as the remaining 5 are unrelated). A snapshot of the **C** matrix is provided in Table 2, in which preferential pairing is declared using pairwise elements (marked in bold) between ramets of respective clones. This structure ensures that the distance among ramets of the same clone is maximized, whereas the distances between preferentially selected clones is minimized. The particular choice of values in the **C** matrix depends on the relative importance assigned to preferential mating to facilitate PAM as opposed to the levels of separation to minimize inbreeding due to selfing. In the fourth scenario, a proportional deployment of clones is used, where the number of respective ramets for each of the 20 clones are as follows: “1-1-2-2-3-3-4-4-4-5-5-6-6-6-7-7-8-8-9-9”. Finally, in the fifth scenario, 5 unrelated groups were considered, each consisting of 3 half-sibs and their respective mother.

Design Comparison

To evaluate the relative superiority of the QAP design to that of the permuted neighborhood and/or the complete randomized counterparts, we derived a proxy to potential inbreeding (selfing in this case) and termed it as “minimum distance” estimate as

$$d_{\min} = \sum_{l=1}^C \sum_{i=1}^K \sum_{j=i+1}^K \frac{1}{d_{i,j}^2} \quad (8)$$

Table 1. Input parameters corresponding to the five illustrated scenarios

Scenario	n_R	Pedigree Structure
1	5	20 unrelated clones
2	5	10 pairs of clones from half-sibs offspring
3	5	20 unrelated clones*
4	1-9	Proportional 20 unrelated clones
5	5	5 unrelated groups: parent and clones from 3 half-sib offspring

* Preferential positive assortative mating. n_R is the number of ramets per clone.

Table 2. Upper triangular elements of the C matrix for 5 ramets of the first 2 clones (clone number followed by the ramet number)

	1-2	1-3	1-4	1-5	2-1	2-2	2-3	2-4	2-5
1-1	50	50	50	50	150	100	100	100	100
1-2		50	50	50	100	150	100	100	100
1-3			50	50	100	100	150	100	100
1-4				50	100	100	100	150	100
1-5					100	100	100	100	150
2-1						50	50	50	50
2-2							50	50	50
2-3								50	50
2-4									50

Bold indicates preferential pairing.

where d is the distance between the i th and the j th ramet of the l th clone, C is the number of clones, and K is the number of ramets within a clone.

Because distance among ramets of the same clone is considered as the major factor for promoting selfing (Erickson and Adams 1989), we used the d_{\min} as a proxy to potential inbreeding (selfing in this case). The d_{\min} represents the inverse sum of squares of all possible distances between any two ramets of the same clone and across all clones. The closer the distance between any two ramets of the same clone, the higher the value and, conversely, the further the distance, the lower the value. Because the COOL and complete randomized designs are only suited for randomizing unrelated clones, we used an orchard with 20 clones each with 5 ramets/clone for comparison. A total of 30 different possible layouts were generated for each of the COOL and complete randomized designs and their average minimum distances were estimated (see Figure 1.C, for a sample COOL design). For the MI design, only one optimum design is produced (Figure 1.1). All designs, which were subjected to the comparison, are available from the corresponding author, along with our computer code (R script) to calculate the d_{\min} .

Results

The minimum distance among the 30 COOL and complete randomized designs produced d_{\min} of 12.53 ± 0.50 (the average \pm half-width of the 95% confidence intervals) and 22.56 ± 1.12 , respectively, compared with 6.82 for the MI optimum layout (scenario 1, Figure 1.1). In addition, the level of dispersal among ramets of the same clone differed (Figure 1.C and 1.1, shaded cells, for example) and, as expected, they were dispersed as far from each other as possible in the MI design (Figure 1.1) compared with COOL (Figure 1.C) and complete randomized designs (not shown), ensuring minimum mating among ramets of the same clone (i.e., selfing). It should be noted that there are no fixed neighborhood effects, a major limitation of the systematic groups of seed orchard designs (Giertych 1975). In addition, the major difference between the MI and the permuted neighborhood design is the lack of exclusion zone in the QAP design, in which ramets of the same clone are separated from each other without any declared distance limitation.

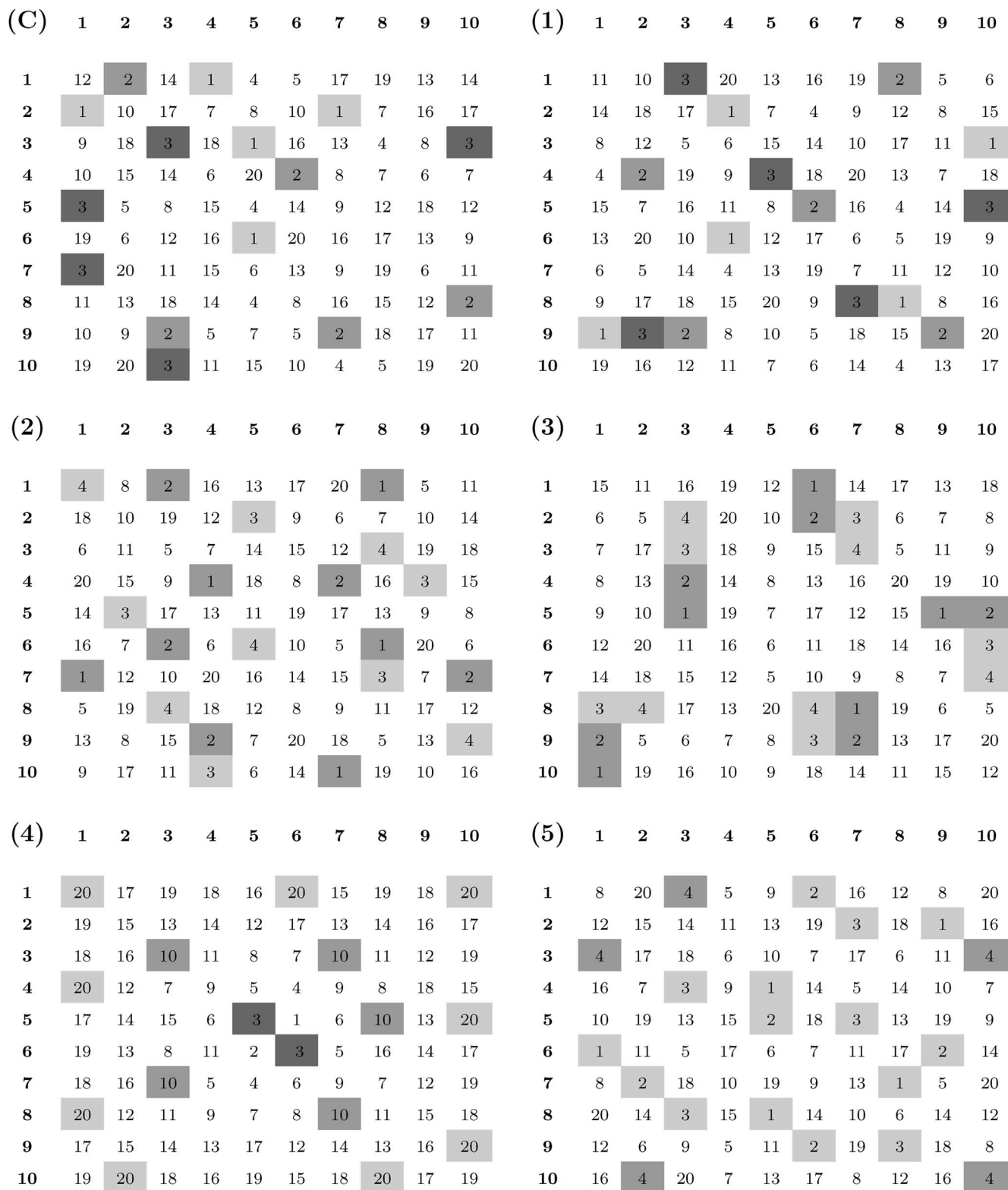


Figure 1. Layout of orchard (20 clones with a 10 × 10 grid): C, permuted neighborhood design (COOL, 20 unrelated clones, each with 5 ramets); 1–5 correspond to the MI design, scenarios 1–5 (Table 1).

Scenario 2 (half-sibs) resulted in the separation of related clones in the orchard, where clones 1 and 2 (related half-sibs) never occur as direct neighbors. The same is true with the remaining pairs of clones (Figure 1.2, shaded cells, for example). There are only two occurrences of diagonal neighbors of related clones in the whole orchard (clones 3

and 4: positions 3–8/4–9 and clones 7 and 8: positions 8–6/9–6) (Figure 1.2). Within this framework, the dispersion of individual ramets of each clone is maximized, and, as in scenario 1, there are no visible neighborhood effects.

In scenario 3 (preferred mating), clones 1 and 2 always appear as close neighbors. The same holds for the remaining

four pairs of clones with declared preferential mating concurrently, whereas the dispersion of ramets of a given clone in the orchard is maximized (Figure 1.3, shaded cells, for example).

In scenario 4, allocation of trees under the proportional deployment scenario resulted in shifting underrepresented clones toward the orchard center (e.g., clones 1 and 2), whereas the overrepresented clones appear at the orchard's edge (e.g., clones 19 and 20) (Figure 1.4, shaded cells, for example). The number of nonzero elements in the objective function grows rapidly with the number of ramets; therefore, the importance of dispersing ramets of the same clone as far apart from each other as possible is highlighted with overrepresented clones (compare the allocation of ramets in clone 3 and 20). As per the three previous scenarios, the minimization of the objective function ensures the attainment of minimum expected inbreeding in the orchard's seed crop.

Finally, in scenario 5, in which three aspects of genetic relationships exist, the resulting layout considered dispersion of individual ramets of each clone, separation of parents from their respective progeny (parent-offspring mating: clone 4 is parent of 1–3, clone 8 of 5–7, clone 12 of 9–11, clone 16 of 13–15, and clone 20 of 17–19), and separation among half-sibs (Figure 1.5, shaded cells, for example). Visual inspection of the resulting layout indicates that the first two considerations are fulfilled, resulting in limiting the available space to meet the third (receiving the lowest weight in the objective function); therefore, half-sibs may appear as neighbors, collectively ensuring minimum expected inbreeding, given the three relatedness layers.

Discussion

Giertych (1975) compared various orchard layouts in terms of their suitability for different purposes. Here, we extend the discussion to the MI design, assuming his original criteria. As indicated in the previous section, the method used in developing the MI design should always yield a clonal arrangement conducive to reaching the expected minimum inbreeding in the orchard's seed crop. The word "expected" suggests that the layout is, strictly speaking, optimum with respect to the information provided during the orchard's establishment. Under more complex schemes (such as scenario 5), there may not be feasible solutions to reach complete avoidance of mating among relatives; however, the optimum solution should lead to the minimum inbreeding of all solutions.

Because there is no predefined arrangement in rows or columns, the MI design does favor panmixis (random mating), as evident from the lack of excessive grouping(s) of relatives (full sibs) originating from certain orchard parents, unless preferentially demanded (scenarios 3 and 4). The MI design is expected to provide an optimum solution considering all input information before design and establishment; thus, changes to the "original" design might be perceived as incompatible with the QAP concept. Natural tree mortality and intentional genetic thinning (removal of clones with low breeding values) or systematic thinning (removal of a subset of trees occupying specific positions to improve spacing as

trees grow) could affect the MI design; however, the random nature of mortality or genetic thinning is expected to have a minimal impact on the design efficiency. However, the lack of repetitive grouping along the orchard's grid might affect the optimal nature of the design if practices such as systematic thinning are contemplated. In these cases, such practices should be considered during the orchard's planning and establishment phases. Although the MI layout could be restrictive to later expansion, it is not restricted to a particular shape and in fact any orchard configuration and spacing variation can be considered. Missing plots (planting positions) or entire rows/blocks of any shape or size can also be included while the **D** matrix was calculated. The design is also flexible and can accommodate a variable number of clones with variable size (number of ramets) as well as multiple forms of genetic relationships. Additional information can be used in forming the **C** matrix (flowering synchronization, breeding values, variability in pollen production, and others) in a manner similar to that described in scenario 3.

The global assignment, as presented here, is flexible for accommodating additional variables, and, at the same time, it is not restricted to some of the assumptions associated with the examples (scenarios). First, mating success may not be necessarily linearly related to the distance. In fact, the method is not constrained by such an assumption. Theoretically, any distribution could be used to describe the relationship. The matrix of distances can be suitably transformed. We do not treat these specific situations here, as there are infinite numbers of possibilities. It should also be noted that real distributions (based on experimental data) could be used in the same manner. Second, we demonstrated the use of the **C** matrix for the preferential pairing. Using this same approach, flowering synchronization data could facilitate better allocation of clones. Mathematically, the approach is the same and should be understood from the formulation in Table 2. In terms of interactions among these factors (e.g., genetic relationship and flowering synchronization), one needs to set proper weights in the **C** matrix. A simple guide is to envision the relative importance of weights in the matrix (such as in the genetic relationship, where 0.5 has a 2 times higher importance in the resultant separation as opposed to the relationship of 0.25). Third, we selected a relatively simple example with an orchard grid of 10×10 . We expect similar trends under different configurations (sizes). There are circumstances when the difference in d_{\min} among the designs would be minimum, e.g., large number of unrelated clones used in similar proportions where each clone is represented by very few ramets. We could also envision cases when the difference in d_{\min} is larger than here.

Exact methods for the QAP have been developed and were proven to be successful in finding the optimum solutions for large problem sizes. In forestry, the number of planting positions in seed orchards can be high. This situation resembles some industrial applications, in which large problem sizes are often encountered, stimulating the development of metaheuristic methods. Because of advancements in optimization theory and computing power, good solutions to very large and difficult QAPs have become

available (Drezner et al. 2005). Various complexity-rating measures have been proposed to assess the difficulty of a given QAP (e.g., Gupta and Deisenroth 1981). One of them is the flow dominance (SD of the elements in **C** normalized by the average). The same measure can be calculated for **D**, denoted as the distance dominance. Generally, the higher the dominance measure, the harder the problem is for local searches. In all scenarios considered in this study, the flow dominance was one-fourth of the distance dominance. Whereas locations (seed orchard grid) were fixed (**D** constant throughout all scenarios), addition of extra layers of genetic relatedness resulted only in a negligible increase in the flow dominance. Therefore, one could assess the complexity of all scenarios considered in this study (in terms of the optimization used) to be approximately the same. In a given application of the MI seed orchard design, the problem size can therefore be considered as the single most important factor influencing the problem complexity. Specific measures should be used under excessively larger problem sizes. One is to consider separate blocks solved independently, with separation borders developed accordingly. However, based on the consistent development, it can be expected that metaheuristic algorithms to QAP will continue to improve, resulting in very large solvable problems (Burkard et al. 2009). Although the optimization is non-trivial for nonmathematicians, the preparation of standardized input is rather intuitive. Optimization software is usually designed to read in the standardized input (matrices **C** and **D** described earlier).

We presented how the MI design works under simplifying assumptions. Any particular crop in a seed orchard is unique, and gametic contributions vary and depend on genetic as well as environmental causes. None of the designs (including the MI) can be fully optimized to accommodate each year's variation in the orchard's reproductive biology. Designs are created to accommodate seed supply over the orchard's lifespan in the best way possible. Our optimality criterion is the minimum inbreeding, referring to the average seed yield in an average year. With regards to the efficiency (d_{\min} used as a proxy to inbreeding), MI design leads to a much greater dispersal, on both the local and global level, with no predetermined fixed exclusion zones. MI design has the advantage of minimizing local groupings of related individuals and should therefore lead to a substantial reduction in inbreeding under most circumstances (majority of distributions). Breeders can calculate the relative efficiency of the MI design based on the specific set of assumptions in a given situation.

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