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Genetic Gain and Diversity Caused by Genetic Thinning in a Clonal Seed Orchard of *Pinus densiflora*

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Abstract

Estimates of genetic gain (in volume growth) and diversity (expressed as status number, N_s) were determined after the application of genetic thinning in a *Pinus densiflora* clonal seed orchard. The genetic thinning was based on: 1) clonal breeding values (represented by general combining ability, *GCA*) obtained from progeny tests, 2) clonal fertility estimated by strobilus production, and 3) clonal size variation determined by the ramet numbers per clone. Genetic gain and diversity estimates were determined under assumptions of 30% pollen contamination and inferior genetic value of contaminating pollen. Thinning 45% of seed orchard (from 67.5 to 41.9 ramets/clone) raised genetic gain to 6.3% in volume growth and reduced the status number to 28.1% of the census number. Further volume growth gain of 11.6% and diversity reduction (N_s = 29.2%) were attained after 70% thinning (from 41.9 to 24.8 ramets/clone). The orchard clones were grouped into 10 *GCA* groups to allow for the linear deployment of clones (i.e., clones were deployed in proportions that reflect their gain estimated), which was implemented for the six top groups. Some ramets from lower groups were intentionally left or removed to avoid the creation of wide gaps or clumps. The effect of pollen contamination on the genetic gain and the consequence of genetic thinning for seed production in the clonal seed orchard were also discussed.

Key words: genetic gain, status number, roguing, *Pinus densiflora,* pollen contamination.

Introduction

Genetic improvement is defined as a process that enhances the genetic value while giving deliberate consideration to the genetic diversity of deployed materials (KANG *et al.,* 2001a). The calculations of genetic gain and diversity in seed orchard populations are of great theoretical and of practical importance. Knowledge of such genetic parameters is essential in the determination of the genetic composition and design of seed orchards as well as the ability to assess the factors influencing genetic quality of orchards' seed. Additionally, it should be realized that clonal genetic value, relatedness among orchard clones, clonal fertility, and pollen contamination, all strongly affect the genetic gain and diversity of orchard seed crops (LINDGREN and MULLIN, 1998).

Seed orchards represent the seed production populations in which the genetic gain attained from tree improvement programs is packaged and delivered to the field foresters in the form of genetically improved seed. Genetic gain of seed orchard crops is realized from the general combining ability (*GCA*) of the selected trees, which comes from the additive variance in the reference/breeding population (KANG, 2001). Seed orchard evolution/advancement overtime (i.e., from first to second and/or advanced generations) is expected to deliver higher gains. These gains parallel the advancement of selection-breeding-testing cycles. Due to the long time required for seed orchards to reach their optimum seed production and the high cost associated with their establishment, the rate of seed orchards generation turnover is often lagging behind that of breeding generations and different strategies were proposed to overcome this limitation (WILLIAMS and ASKEW, 1993).

Genetic gain in the first-generation seed orchard, on the other hand, is unpredictable due to the untested nature of the orchard clones/families. These clones/families were included in the production populations mainly based on their phenotypes. As breeding and testing information becomes available, the necessity of genetic upgrading in the seed orchard population becomes important. The most common practice applied for this genetic upgrading is the implementation of genetic thinning (i.e., roguing). In most cases, genetic thinning is implemented after several years of seed orchard establishment. Thus, the available information on the orchard clones/families such as genetic value, fertility, and reproductive phenology as well as

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the observed overall level of pollen contamination should be used as valuable foundation for genetic thinning decisions.

In Korea, the breeding program for *Pinus densiflora* was initiated in 1959. Plus-trees have been selected through the natural range of the species and tested by means of open- and control-pollinated progeny tests (HAN *et al.,* 1997). Additionally, a total of 99 ha first-generation seed orchards of *P. densiflora* are established from 1969. First genetic thinning based on clonal *GCA* value and fertility was conducted in a 32 ha orchard when grafts were 20 years old.

The main objectives of this study are to estimate the changes of genetic gain and diversity caused by genetic thinning of a *P. densiflora* clonal seed orchard and to evaluate the consequences of the genetic thinning on seed production and the management of the seed orchard.

Materials and Methods

Genetic thinning

The studied 32 ha *P. densiflora* seed orchard is located in Anmyon island, western part of Korea (lat.: 36°3'N, long.: 126°2'E and elev.: 35m) and was established in 1977. A total of 192 clones (total 12,833 ramets) were included at establishment. The average number of ramets per clone at establishment was 66.8 (range: 1 to 449 ramets/clone). See KANG (2000) for more detailed information regarding the seed orchard and the assessment of strobilus production.

Two genetic thinning treatments were carried out, which involved the removal of 45 and 70% of the orchard trees in 1996 and 1999, respectively. Genetic thinning was carried out utilizing the genetic information generated from the open-pollinated progeny tests and clonal fertility (i.e., flowering assessment that considered clonal size). Clonal fertility has been monitored and assessed yearly. For the analyses presented below, the few clones that were not monitored were given flowering value that equals to the grand mean of seed orchard flowering. Since selection criteria for genetic thinning were based on clonal genetic values and flower production, clones with inferior general combining abilities (*GCA*) and poor seed production were targeted for ramet removal more than superior clones.

Volume growth *GCA* for each clone was estimated using the best linear unbiased prediction (BLUP) method. Details on the genetic testing and estimation procedure are documented in HAN *et al.* (1997). Clones were divided into 10 classes, based on their *GCA* values, to monitor the deployment of orchard clones before and after genetic thinning.

Genetic gain

Genetic gain is the average of the genetic values of female and male parents. In the presence of pollen contamination, the genetic value of male parent is reduced due to the inferiority of contaminating pollen. Genetic gain (ΔG) was estimated (cf., GRIFFIN, 1982) as follows,

$$\Delta G = \sum_{i=1}^{N}\left(\frac{GCA_{female}+GCA_{male}}{2}\times q_i\right) = \sum_{i=1}^{N}\left(\frac{GCA_{fi}+\{(1-2M)GCA_{mi}+(2M)GCA_{mc}\}}{2}\times q_i\right)$$

where GCA_{fi} and GCA_{mi} are general combing abilities of orchard female and male parents of the i-th clone, GCA_{mc} is the general combing ability of contaminating pollen, M is the rate of gene migration (i.e., half of pollen contamination), and q_i is the relative frequency of i-th clone, which considers ramet number and seed production.

Status number

Genetic diversity was measured by status number (N_s) that was defined as half the inverse of group coancestry by LINDGREN *et al.* (1996). For unrelated and non-inbred orchard clones, N_s can be estimated from the contribution of the clones. The status number was calculated (cf., KANG and LINDGREN, 1998) as,

$$N_s = \frac{1}{\sum_{i=1}^{N}(p_i\times r_i)^2} = \frac{1}{\sum_{i=1}^{N}\left(\frac{f_i+(1-2M)m_i}{2}\times r_i\right)^2} = \frac{4}{\sum_{i=1}^{N} f_i^2 r_i^2 + (1-2M)^2\sum_{i=1}^{N} m_i^2 r_i^2 + 2(1-2M)\sum_{i=1}^{N} f_i m_i r_i^2}$$

where p_i is the contribution of the i-th clone, f_i and m_i are the contributions of females and males of the i-th clone and r_i is the ramet proportion of the i-th clone.

Note that there is a large variation of ramet number (r_i) among the orchard clones, and thus the ramet variation should be considered and weighted to calculate the status number and the genetic gain (NIKKANEN and RUOTSALAINEN, 2000; KANG *et al.,* 2001b).

Assumptions

In the present study, the rate of pollen contamination was set to 30% (M = 0.15) and an additive variance of contaminating pollen (GCA_{mc}) was assumed to be –0.1. The assumption was based on the review of pollen contamination (SAVOLAINEN, 1991; ADAMS *et al.,* 1997; KANG, 2001). ADAMS *et al.* (1997) pointed out that levels of pollen contamination could exceed 30–40% even in mature seed orchards with heavy pollen production. The negative value of GCA_{mc} means that the genetic value of contaminating pollen is, on average, 10% inferior in volume growth relative to the orchard pollen. It was also assumed that *GCA* and seed production were independent traits.

Plus tree selection, by definition, assumes that the genetic relatedness (i.e., coancestry) among selected trees does not exist and thus the orchard clones are neither related nor inbred. It was assumed that there was no relatedness among orchard pollen and contaminating pollen, and within contaminating pollen itself. The degree of relatedness within a breeding program depends on the number and size of generation turnover. However, tree breeding is still under the very early stages of domestication and thus it is reasonable to assume no relatedness among orchard clones in the first-generation seed orchards.

Results

Genetic gain

At stage of establishment, the initial theoretical genetic gain of seed orchard crop was estimated to be negative (–0.03%). Note that the initial theoretical gain should be the same as the genetic value of contaminating pollen, $\Delta G = GCA^{mc} = -0.1$. However, the actual unbalanced ramet number and fertility variation among clones raised the expected genetic gain to 0.07% (*Table 1*). As expected, estimates of genetic gain and relative status number increased by genetic thinning. Genetic thinning levels of 45 and 70% increased the volume growth gain by 6.3 and 11.6%, respectively (*Table 1*).

The knowledge of clonal *GCA* value and fertility was utilized during tree removal. So, clones with high *GCA* maintained proportionally more ramets than clones with low *GCA* (i.e., linear deployment). This linear deployment was more pronounced after grouping the orchard clones in 10 classes on the basis of

Table 1. – Census number (N: number of clones), ramet number (n), genetic gain (ΔG) and status number (N_s) at the establishment of seed orchard and after the implementation of 45 and 70% genetic thinning in a clonal seed orchard of *Pinus densiflora*.

	Initial establishment	1st genetic thinning (45%)	2nd genetic thinning (70%)
N	190	172	161
n	12,830	7,207	3,999
(mean/clone)	(67.5)	(41.9)	(24.8)
ΔG (%)	0.07	6.3	11.6
N_s	27.9% of N	28.1%	29.2%

* Pollen contamination was set to 30% and an additive variance of contaminating pollen was assumed to –0.1. Note that ramet variation was considered to calculate genetic gain and status number. Rate of genetic thinning was based on the number of ramets/clone.

their *GCA* ranks (*Fig. 1*). The six high genetic value classes were considered for the linear deployment, yielding the mean number of ramets/class of 1283, 721 and 400 for before and after 45 and 70% genetic thinning, respectively (*Fig. 1*). It should be noted that the numbers of ramets/clone for lower classes (from seventh to tenth classes) were intentionally left or removed in order to avoid the creation of wide gabs or clumps within the seed orchard.

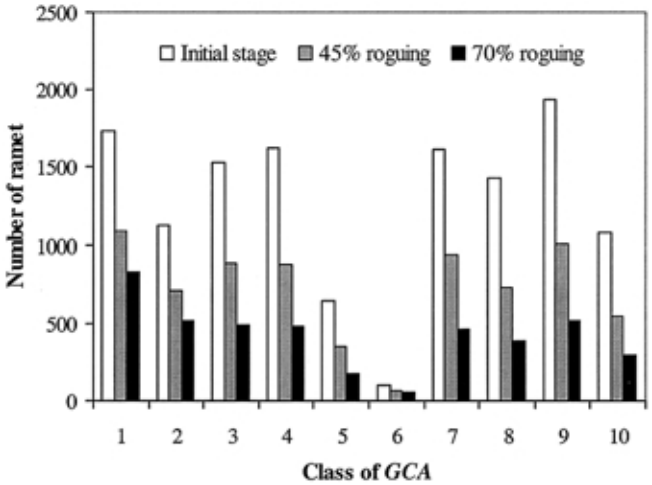

Figure 1. – Number of ramets/clone before and after 45 and 70% genetic thinning by grouping into 10 *GCA* classes in a 32 ha clonal seed orchard of *Pinus densiflora*. Genetic thinning was implemented based on clonal *GCA* values and fertility (seed production). Linear deployment by genetic thinning appeared from first to sixth classes.

Genetic thinning decreased seed production immediately after tree removal, but seed production recovered after a few years (Fig. 2). This substantial recover in seed production was coupled with an overall increasing trend in genetic gain (Fig. 2). Additional gain from this seed orchard is expected to reach 15% after the implementation of final genetic thinning (Fig. 2).

Genetic diversity

The initial status number (N_s) was reduced to 27.9% of the census number due to fertility and ramet variations (*Table 1*). This initial status number should have been even smaller than 27.9% of census number under no pollen contamination scenario. The values of N_s after the application of 45 and 70% genetic thinning were estimated to 48.3 (28.1%) and 47.0 (29.2%), respectively (*Table 1*).

Genetic thinning levels of 45 and 70% maintained the relative status number (% of census number) at more or less constant level of 28.1 and 29.2% vs. 27.9% of the census number (*Table 1*). The main reason for reaching stable status number was the removal of many ramets from lower gain clones while maintaining these clones with a low representation in the seed orchard. The numbers of clones that were totally removed were 18 and 29 for 45 and 70% genetic thinning, respectively (*Table 1*).

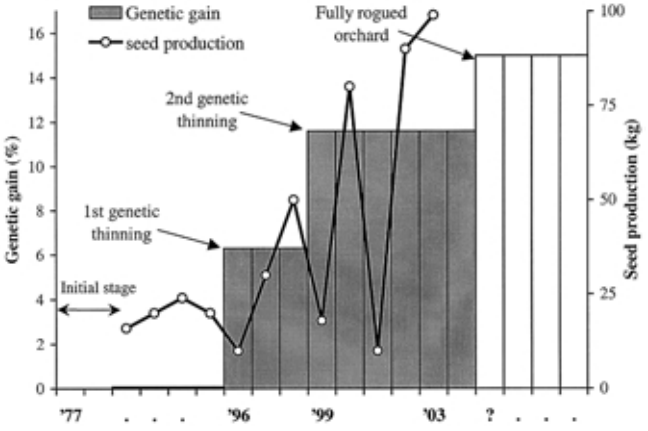

Figure 2. – Changes in genetic gain and seed production by genetic thinning in a 32 ha clonal seed orchard of *Pinus densiflora*. Genetic thinning caused a decrease of seed production immediately after tree removal, but seed production recovered in a few years. Seed production is expected to reach more than 100 kg in 2003.

On average, the number of ramets/clone showed steady decline from initial establishment to after 45 and 70% genetic thinning, yielding averages of 67.5, 41.9 and 24.8 ramets/clone, respectively (*Table 1*). It should be noted that the rates of genetic thinning were calculated on the basis of the numbers of ramets/clone.

Discussion

Genetic thinning of the seed orchard increased the genetic gain and maintained the genetic diversity at acceptable level (*Table 1*). The genetic gain was directly affected by the genetic value of clones and their reproductive contribution. As expected, the status number was reduced (N_s = 53.0 ⇒ 48.3 ⇒ 47.0), due to the fact that the status number is usually smaller than the census number as a by-product of genetic relatedness (i.e., coancestry) which was not operating in the present study, fertility difference and ramet variation among clones (LINDGREN and MULLIN, 1998; GÖMÖRY *et al.,* 2000; KANG *et al.,* 2001b).

It has been generally assumed that gametic contributions among clones are equal when genetic gain and status number are estimated (GRIFFIN, 1982; LINDGREN and MULLIN, 1998). However, GÖMÖRY *et al.* (2000) and KANG *et al.* (2001b) clearly demonstrated that the clonal gametic contributions should be weighted or be proportional to the number of ramets/clone for increasing gain and maintaining diversity. This was also demonstrated in the present study.

The clonal linear deployment concept applied in this study capitalizes on the differential variation of genetic gain among orchard clones (LINDGREN and MATHESON, 1986). It can thus be beneficial to intentionally use an unequal number of ramet per clone, where clones with high breeding value contribute most to the seed orchard crop, thus gain is maximized without appreciable genetic diversity loss (LINDGREN and EL-KASSABY, 1998).

When dealing with unrelated clones with known breeding values, the linear deployment means using a ramet number

directly proportional to the breeding value. This produces possibility to maximize the genetic gain at a given desirable genetic diversity (LINDGREN *et al.,* 1989; BONDESSON and LINDGREN, 1993; HODGE and WHITE, 1993). But, the level of clonal difference in fertility rather than mere ramet number is required for the successful implementation of linear deployment concept (ROBERDS *et al.,* 1991; CHAISURISRI and EL-KASSABY, 1993; EL-KASSABY and COOK, 1994).

Most first-generation seed orchards have been established with an intention to start with near-equal numbers of ramets for each clone. However, this goal is difficult to fulfill and the large variation of ramet numbers among clones always exist due to graft availability, graft incompatibility and different kinds of biotic and abiotic factors (KANG *et al.,* 2001b). When the results of progeny test become available in the form of breeding value or *GCA*, an intentional change in the proportion of ramets among clones occurs by genetic thinning (NIKKANEN and PUKKALA, 1987; BONDESSON and LINDGREN, 1993). Thus, manipulating the number of ramets/clone within seed orchards should be considered when the clonal genetic values and fertility estimates are known and the genetic diversity of seed crops is of importance during seed production.

It is important to point out that there would be fluctuation in seed production even after recovery from tree removal effect. Seed production in 1999 and 2001 showed a reduction after pronounced increase in seed yield. EL-KASSABY *et al.* (1989) presented evidence indicating that lower seed yield is expected specifically after mast years. Anatomically a seed-cone is a modified branch, thus a high seed-cone year reduces the chance for cone baring sites for the following year. On the other hand, EL-KASSABY *et al.* (1989) and others pointed out that seed yield in years following good crops is usually low due to the observed small seed-cone count and/or the increased level of predation from the commonly observed higher insect population levels.

As the seed orchard matures, the implementation of intensive management practices such as selective cone induction of high *GCA* clones, and application of supplemental mass pollination (EL-KASSABY *et al.,* 1989) are expected further increase the genetic gain providing an interim supply of needed genetically improved seed for reforestation programs. This interim seed supply with its acceptable levels of gain and diversity offers a valid alternative to replacing this productive first-generation seed orchard by newly established second-generation orchards. Thus, providing a situation where the breeding program continues to develop its advanced breeding populations while the seed orchard program keeps pace but with the concept of skipping one generation, namely, second-generation seed orchard.

Genetic gain estimated in seed orchards may be over estimated if the unequal contribution by fertility difference and ramet variation is not considered. In advanced-generation seed orchards, relatedness among seed trees would add another factor that needs to be considered when genetic gain and diversity are estimated. In future seed orchards, the orchard clones are selected from trees produced through various mating designs used for breeding and testing phases, then some of the orchard individuals will be sharing common parents. The relatedness level and their inbreeding effects could offset some of the expected gains from the advanced-generation seed orchards (ASKEW and BURROWS, 1993).

In conclusion, the present study has demonstrated the effective use of seed orchard's clonal information. Paramount to this exercise (i.e., genetic thinning) is clonal genetic gain and fertility variation. Effective use of the information secures the usefulness of production populations and their effective use.

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