

Gender, reproductive output covariation and their role on gene diversity of *Pinus koraiensis* seed orchard crops

Ji-Min Park

Seoul National University College of Agriculture and Life Sciences

Hye-In Kang

Seoul National University College of Agriculture and Life Sciences

Da-Bin Yeom

Seoul National University College of Agriculture and Life Sciences

Kyu-Suk Kang (✉ kangks84@snu.ac.kr)

Seoul National University College of Agriculture and Life Sciences <https://orcid.org/0000-0002-2368-5423>

Yousry A. El-Kassaby

University of British Columbia

Kyung-Mi Lee

National Institute of Forest Science

Research article

Keywords: effective population size, fertility variation, flowering assessment, reproductive success, parental balance, Korean pine

Posted Date: August 31st, 2020

DOI: <https://doi.org/10.21203/rs.3.rs-24844/v3>

License: © ⓘ This work is licensed under a Creative Commons Attribution 4.0 International License.
[Read Full License](#)

Version of Record: A version of this preprint was published at BMC Plant Biology on September 7th, 2020. See the published version at <https://doi.org/10.1186/s12870-020-02632-9>.

Abstract

Background: Gender and fertility variation have an impact on mating dynamics in a population because they affect the gene exchange among parental members and the genetic composition of the resultant seed crops. Fertility is the proportional gametic contribution of parents to their progeny. An effective number of parents, derivative of effective population size, is the probability that two alleles randomly chosen from the gamete gene pool originated from the same parent. The effective number of parents is directly related to the fertility variation among parents, which should be monitored for manipulating gene diversity of seed crops. We formulated a fundamental equation of estimating the effective number of parents and applied it to a seed production population.

Results: Effective number of parents (N_p) was derived from fertility variation (Y) considering covariance (correlation coefficient, r) between maternal and paternal fertility. The Y was calculated from the coefficient of variation in reproductive outputs and divided into female (y_f) and male (y_m) fertility variation in the population under study. The N_p was estimated from the parental Y estimated by the fertility variation of maternal (y_f) and paternal (y_m) parents. The gene diversity of seed crops was monitored by Y and N_p in a 1.5 generation *Pinus koraiensis* seed orchard as a case of monoecious species. A large variation of female and male strobili production was observed among the studied 52 parents over four consecutive years, showing statistically significant differences across all studied years. Parental balance curve showed greater distortion in paternal than maternal parents. The Y ranged from 1.879 to 4.035 with greater y_m than y_f and the N_p varied from 14.8 to 36.8. When pooled, the relative effective number of parents was improved as 80.0% of the census number.

Conclusions: We recommend the use of fertility variation (i.e., CV , Y), Person's product-moment correlation (r), and effective number of parents (N_p) as tools for gauging gene diversity of seed crops in production populations. For increasing N_p and gene diversity, additional management options such as mixing seed-lots, equal cone harvest and application of supplemental-mass-pollination are recommended.

Background

Gender and reproductive output variation have a profound impact on the mating dynamics in a population, such as forest tree seed orchards, as they affect the gene exchange among the parental populations' members and the genetic composition of the resultant seed crops (El-Kassaby 1995; Matziris 1997; Burczyk and Chalupka 1997). In seed orchards, the theoretical expectation of reproductive output equality (uniform production of male and female gametes) is hardly fulfilled (Eriksson et al. 1973) and the extent of this variation has been the subject of extensive research (O'Reilly et al. 1982; Griffin 1982; Chaisurisri and El-Kassaby 1993; El-Kassaby and Cook 1994; Adams and Kunze 1996; Ertekin 2010; Song et al. 2018). Quantitative assessment of reproductive output in conifer seed orchards clearly indicated the presence of sexual asymmetry between female and male fertility (El-Kassaby and Cook 1994; Kjær and Wellendorf 1997; Gomory et al. 2000; Ertekin 2010); however, this asymmetry could be

further separated if the observed reproductive output variation is either negatively or positively correlated (i.e., covariation).

Covariance is a measure of the joint variability of both variables (e.g., female and male fertility) in statistical probability theory. If greater values of female fertility correspond with greater values of male fertility, the covariance of female and male is positive. Conversely, when female and male fertilities tend to show opposite behavior, the covariance is negative. The sign of the covariance therefore shows the tendency in their linear relationship. The magnitude of the covariance is not easy to interpret because it is not normalized and hence depends on female and male fertilities magnitudes. However, correlation coefficient (i.e., the normalized version of covariance) shows the strength of the linear relation by its magnitude.

Effective population size (N_e) is one of the key genetic indicators in plant breeding and conservation programs, and it is central to population genetics and evolutionary biology (Frankham et al. 2010; Allendorf et al. 2013). N_e quantifies the magnitude of genetic drift and inbreeding in the population under study. Several theoretical effective number extensions have been made such as inbreeding effective population size $N_e^{(i)}$, variance effective population size $N_e^{(v)}$ (Wright 1931), selection effective population size (Lynch 2007), and status number (Lindgren and Mullin 1998). In practice, N_e is, however, notoriously difficult to estimate. In forestry context, Kang (2000) indicated that the effective number of parents is the number of individuals in which an idealized population would produce the same number of offspring (sibs) as the real population.

Pinuskoraiensis Siebold & Zucc, commonly known as Korean pine, is a coniferous white-pine tree species native to the temperate rainforests of Korea, Japan, and the Ussuri River basin of China and Russia. Primordia differentiation starts in year-1, pollination and fertilization is completed in year-2, and seed and cone development is completed in year-3 (Owens and Fernando 2007). The Korean pine occupies more than 25% of the total forest area in South Korea and is managed for timber and seed production for furniture, construction and human consumption (Kim et al. 2005; Yi 2005; Feng et al. 2011). In South Korea, Korean pine genetic improvement started with the selection of 300 phenotypically superior individuals forming the breeding population in 1959 (i.e., plus-trees) and the establishment of open-pollinated progeny tests in 1975 (Granhof 1991). In 1970, the first-generation seed orchard was established by grafts of the selected plus trees. Volume growth, tree trunk volume, was the main selection criterion used for the transition from first- to 1.5-generation seed orchards (Granhof 1991; Yi 2005). Thus, the 1.5-generation seed orchard represents the second-cycle of the program's seed orchard and superior parents were selected based on their growth characteristics.

Investigating the extent of reproductive output (strobili and seed production) variation and covariation as well as the genetic composition of seed crops are essential to ensure the genetic quality of reforestation stock. However, the reproductive output and success information of *P. koraiensis* seed orchards have been limited. Here, we utilized a 1.5-generation *P.koraiensis* clonal seed orchard to develop a framework for estimating: 1) the effective number of parents (i.e., effective population size) considering the observed

gender and reproductive output variation and covariation and 2) the gene diversity of the orchard's seed crops. To do so, over four consecutive years, we surveyed strobili production difference and correlation of the seed orchard's 52 parents (clones) and investigated gender (female and male strobili production) and reproductive output variation and covariation.

Results

Fertility covariation and effective number of parents

Under various scenarios of female and male fertility covariation (i.e., joint variability of female and male fertility related to correlation), the effective number of parents was stochastically simulated under a range of correlation coefficients ($-1.0 \leq r \leq 1.0$) (Fig. 1). Generally, under no or limited female and male parents reproductive output fertility covariation, the effective number of parents (N_p) was always equivalent to the census number (N) as the seed orchard parents are unrelated and assumed to be non-inbred (Fig. 1).

Positive female and male parents reproductive output fertility covariation increased the sibling coefficient (Y ; parental fertility variation) as Y is affected by variation in both female (y_f) and male (y_m), causing the effective number of parents (N_p) declined (Fig. 1.a – 1.d), compared to equal fertility with no correlation. On the other hand, negative female and male parents reproductive output fertility covariation mitigated the asymmetrical variation between y_f and y_m (fertility variation imbalance), resulting the incremental increase of the effective number of parents (Fig. 1.e – 1.i).

Knowledge regarding the extent of gene diversity loss (GD) when genes are transmitted from orchard parents to their progeny is valuable. The GD is estimated using Eq. (8) for new seed orchard establishment plans. If 5% loss of gene diversity is tolerable, then the effective number of parents N_p of 10 would be sufficient in providing the desired seed crop's gene diversity (Fig. 2). However, striving to reach higher effective number of parents is preferable to ensure capturing reasonable level of gene diversity.

Case study: *Pinus koraiensis* seed orchard

The average number of female strobili per ramet (a member of a clone) fluctuated across the studied years, with 2015 and 2016 representing the highest and lowest production with clone averages of 2.99 and 0.33, respectively (Table 1). The clonal average number of male strobili over years produced striking differences with 2017 and 2014, showing the highest and lowest production with averages of 1,912.2 and 1.82, respectively (Table 1). The female and male strobili production over the studied years was low and negating panmixia expectations in the 1.5 generation clonal seed orchard of *P.koraiensis*. This was similar situation with previous observation in the first-generation clonal seed orchards of the same species.

The effective number of female parents ($N_p^{(f)}$) was higher than that of male parents ($N_p^{(m)}$) except in the year 2017 (Table 2, Fig. 3). The relative effective number of female parents ranged 45.9% in 2016 (poor

year) to 85.5% in 2014 (good year), and the expected loss of gene diversity (GD) for female and male parents were 1.1% and 1.6%, respectively, which was not so alarming for a 52 clonal seed orchard (Table 2). The clonal effective number of parents (N_p) under female and male strobili production covariation varied between 14.8 and 36.8 for 2014 and 2017 across the four studied years (Table 3) where N_p was calculated using the CV and r of female and male strobili production (see Equation 6). The seed crops' loss of gene diversity (GD) varied between 3.4% and 1.4% for 2014 and 2017, presenting higher than expected values for female and male parents and indicating the effect of covariation (correlation) between female and male fertility.

The parental balance curves showed that clonal cumulative gamete contribution was far from expectation (i.e., equal contribution) specifically for 2016 female and 2014 male (Fig. 4). The male strobili production cumulative curves showed greater distortion than that for female. The top 20% of clone contributed 59.6% of female strobili production (2016) while 86.4% of male production (2015). On the other hand, male strobili production was limited to extremely limited clones as only two clones contributed 50% of total production (Fig. 4).

Parental contribution as males, females or both sexes should influence the seed crop's genetic composition, and this can be determined with assessment of the orchard's initial reproduction and throughout the cone crop development. The current study indicated that there were 8 clones (15.4%) consistently ranked high on the gametic contribution. On the other hand, 8 clones were persistently ranked low across the orchard reproduction years, which could contribute to the needed reproductive output assessment. The genetic worth of orchards' seed crops is a function of parental gametic contribution and their respective breeding value, thus sibling coefficient could be one of the criteria needed for evaluating the genetic composition as it determines parental gametic contribution (Kang 2000). Large variation among orchard parents' gametic contribution is common and widely reported in many seed orchards (Funda and El-Kassaby 2012). Thus, an evaluation of seed crops' genetic composition should consider the entire parental population as an analytical unit of gametic and genetic contribution.

By knowing the magnitude of fertility variation among individuals in a seed orchard, the census number to collect seed-cones could be chosen to achieve satisfactory gene diversity of seed crops (Kang et al. 2003). We exposed the practice of equal seed-cone harvest for a good crop year (2015) in the *P. koraiensis* seed orchard. The equalizing of female fertility should be preferentially set to the most-fertile female parents, and the male fertilities were not changed. When the proportion of equal seed-cone harvest increased, the effective number of parents increased, but the relative seed-cone production was decreased when compared to the commercial harvest (Fig. 5).

Discussion

Fertility variation and effective number of parents

Each gamete produced by a diploid tree only harbors one allele of each gene, which is chosen at random from the tree's two copies. Under Mendel's law of segregation, each of the two alleles in the tree has an equal probability of being included in a gamete. However, the probability is expected to change due to the present fertility variation between female and male parents. The sibling coefficient (Y) describes the fertility variation in the population under study as it is derived from the variances of female and male fertility (i.e., coefficient of variation, CV_f and CV_m). It does not depend on the genealogical relationship between parents (i.e., related or otherwise: Kang 2000). When all parents, female and male, contribute equally ($Y = 1$), which is proportionate to census number ($1/N$), then the situation of covariance (Fig. 1) is similar to the no covariation as described in Scenario A. The Y can also describe the expected increase of inbreeding (i.e., loss of gene diversity) in the seed crops following random mating.

If there is no gene migration (gene flow from outside the orchard), the inbreeding in the following generation will be equal to $Y/(2N)$, which is the probability that uniting gametes are identical-by-decent in a random mating population (Falconer and Mackay 1996). In a seed orchard of bisexual species, *Pinustabuliformis*, and over surveyed years, Li et al (2011) reported the presence of significant positive and negative correlations between female and male parents' contributions. Such correlations should be taken into consideration when the gene diversity of seed crop is estimated because maternal and paternal contribution covariation would mitigate or boost the difference of gametic contribution between gender as shown this study.

The effective number of parents (N_p) is expected to be equivalent to the status number (N_s) if the population members are non-inbred and unrelated (Lindgren et al. 1996; Lindgren and Mullin 1998; Gomory et al. 2000; Kang et al. 2004). The N_p is a derivative of effective population sizes to estimate gene diversity in the real population, which considers the variance of contribution (fertility variation) among parents. Gene migration (pollen flow/contamination from outside sources) is expected to increase N_p and gene diversity but decrease orchard crops' genetic worth (El-Kassaby and Ritland 1986a,b; El-Kassaby et al. 1993; Harju 1995; Lindgren and Mullin 1998; Sønstebø et al. 2018). It is worth noting that gene migration only affects a portion of the male contribution, which represents half of the seed crops' parental input.

Manipulating reproductive output variation through crop management

The reduced effective number of parents and the presence of common parentage (i.e., relatedness among clones) are expected to increase the inbreeding in the resulted seed crops. The parental distortion (i.e., fertility variation) was improved and in turn the effective number of parents was increased. when all crops are pooled across the four-years, indicating that mixing seeds from several years could be beneficial in enhancing gene diversity. While the number of female and male strobili is an indication of gametic contribution among the orchard parents, it should be stated that this assumption can be affected by other factors such as reproductive phenology variation, pollen dispersal distances, pollen viability and competition, self-compatibility, male-female complementarity and/or frequency-dependent male

reproductive success as well seed viability and germination (El-Kassaby and Reynolds 1990; El-Kassaby et al. 1992; Chaisurisri et al. 1992; Kjær and Wellendorf 1997).

Implementation of equal seed-cone harvest caused a substantial loss of seed production (Fig. 4). Thus, a trade-off between seed production and the effective number of parents (gene diversity) should be carefully considered. The fertility from over-represented female parents would be the most concern in the equalizing maternity in seed orchards (Burczyk and Chalupka 1997; Kang and El-Kassaby 2002). The trade-off between gene diversity and seed collection would be more important in the *ex-situ* gene conservation program of genetic resources (Kang et al. 2003).

Maternal, paternal, and parental (clonal) contribution can be appropriately estimated by analysis of reproductive output and correlation (covariation) between female and male parents across individuals in a seed orchard. In turn, gametic and genetic contribution of individuals to their seed crops can be calculated (Li et al. 2011). To alter the genetic composition of orchards' gene pools and improve the genetic worth of their resulting seed crops, intrusive management options can be applied during cone crop development. To effectively manipulate the gene pool, orchard crops' genetic composition needs to be predicted to assist the decision-making process and the selection of the appropriate management option to implement (e.g., genetic thinning, selective cone harvest: Lindgren and El-Kassaby 1989; Li et al. 2011).

Conclusions

We recommend the use of fertility variation (i.e., CV and Y), Person's product-moment correlation (r) and effective number of parents (N_p) as tools for gauging seed orchard crops' gene diversity. The effective number of parent (N_p) is a characteristic of the seed crops derived from unequally contributing parents. This could be extended to orchard parents in advanced generation seed orchards (or breeding populations) because the N_p does not depend on the relatedness of parents but solely on the fertility variation.

The present study highlighted the presence of some obstacles with female fertility (seed production) and gene diversity loss in the studied 1.5-generation *Pkoraiensis* clonal seed orchard, which were mainly associated with large fertility variation, inadequate pollen supply, panmictic disequilibrium, and parental unbalance. Thus, the implementation of seed-cone crops management alternatives such as equal seed-cone harvest among clones and/or supplemental-mass-pollination could be effective options in improving the parental balance and the crop's genetic worth, and increasing the gene diversity.

Methods

Due to technological limitations, the Methods section is only available as a download in the supplementary files.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent to publish

Not applicable.

Availability of data and materials

The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Competing interests

The authors declare that they have no competing interests.

Funding

KS Kang and JM Park got the funding that was supported by the R&D program of the Korea Forest Service (Korea Forestry Promotion Institute Project No. 2020182B10-2022-BB01). KS Kang designed the study, interpreted the data, and wrote the manuscript together with JM Park.

Author's contributions

JM, HI, DB and KM collected and analyzed the phenotypic data and wrote the manuscript under the supervision of KS and YAE. KS designed work and obtained funding and YAE revised the manuscript. All the authors participated in revising it critically and gave approval of the final version to be submitted.

Acknowledgement

Authors thank the National Seed Variety Center of the Korea Forest Service for kind permission of data collection in the seed orchard. This study was partially completed while KS Kang was a visiting faculty to the Department of Forest and Conservation Sciences, Faculty of Forestry, The University of British Columbia, Canada.

References

1. Adams GW, Kunze HA. Clonal variation in cone and seed production in black and white spruce seed orchards and management implications. *For. Chron.* 1996;72:475-480.
2. Allendorf FW, Luikart GH, Aitken SN. Conservation and the Genetics of Populations. John Wiley and Sons: Chichester, West Sussex, UK, 2013.

3. Bilir N, Prescher F, Ayan S, Lindgren D. Growth characters and number of strobili in clonal seed orchards of *Pinus sylvestris*. *Euphytica* 2006;152:293-301.
4. Burczyk J, Chalupka W. Flowering and cone production variability and its effect on parental balance in a Scots pine clonal seed orchard. *Ann. Sci. For.* 1997;54:129-144.
5. Chaisurisri K, El-Kassaby YA. Estimation of clonal contribution to cone and seed crops in a Sitka spruce seed orchard. *Ann. Sci. For.* 1993;50:461-467.
6. Chaisurisri K, Edwards DGW, El-Kassaby YA. Genetic-control of seed size and germination in Sitka spruce. *Silvae Genet.* 1992;41:348-355.
7. El-Kassaby, YA. Evaluation of the tree improvement delivery system: Factors affecting the genetic potential. *Tree Physiol.* 1995;15:545-550.
8. El-Kassaby YA, Barnes S, Cook C, MacLeod DA. Supplemental-mass-pollination success rate in a mature Douglas-fir seed orchard. *Can. J. For. Res.* 1993;23:1096-1099.
9. El-Kassaby YA, Cook C. Female reproductive energy and reproductive success in a Douglas-fir seed orchard and its impact on genetic diversity. *Silvae Genet.* 1994;43:243-246.
10. El-Kassaby YA, Edwards DGW, Taylor, DW. [Genetic-control of germination parameters in Douglas-fir and its importance for domestication](#). *Silvae Genet.* 1992;41:48-54.
11. El-Kassaby YA, Reynolds S. Reproductive phenology, parental balance and supplemental mass pollination in a Sitka spruce seed orchard. *For. Ecol. Manage.* 1990;31:45-54.
12. El-Kassaby YA, Ritland K. Low level pollen contamination in a Douglas-fir seed orchard as detected by allozyme markers. *Silvae Genet.* 1986a;35:225-229.
13. El-Kassaby YA, Ritland K. The relation of outcrossing and contamination to reproductive phenology and supplemental mass pollination in a Douglas-fir seed orchard. *Silvae Genet.* 1986b;35:240-244.
14. Eriksson G, Johnsson A, Lindgren D. Flowering in a clonal trial of *Picea abies* Stud. For. Suce. 1973;110:4-45.
15. Ertekin M. Clone fertility and genetic diversity in black pine seed orchard. *Silvae Genet.* 2010;59:145-150.
16. Feng FJ, Zhao D, Sui X, Sun XY. Study on mating system of *Pinus koraiensis* in natural population based on cpSSR technology. *Advanced Materials Research* 2011;p183-185;700-704.
17. Frankham R, Ballou JD, Briscoe DA. *Introduction to Conservation Genetics*, second ed. Cambridge University Press, Cambridge, UK.
18. Funda T, El-Kassaby YA. Seed orchard genetics. *CAB Reviews* 2012;7.23pp.
19. Funda F, Liewlaksaneeyanawin C, Fundova I, Lai BSK, Walsh CG, Van Niejenhuis A, Cook C, Graham H, Woods J, El-Kassaby YA. [Congruence between clonal reproductive investment and success as revealed by DNA-based pedigree reconstruction in conifers seed orchards](#). *Can. J. For. Res.* 2011;41:380-389.
20. Gomory D, Bruchanik R, Paule L. Effective population number estimation of three Scots pine (*Pinus sylvestris*) seed orchards based on an integrated assessment of flowering, floral phenology

- and seed orchard design. *For. Genet.* 2000;7:65-75.
21. Granhof J. Mass production of improved material, 2: Seed orchards: Concepts, design and role in tree improvement. Danida Forest Seed Centre, Humlebaek, Denmark. Lecture Note D-8, Uden navn, 1991.
 22. Gregorius H. Characterization and analysis of mating system. Ekopan Verlag, Germany, 1989.
 23. Griffin AR. Clonal variation in radiata pine seed orchards. I. Some flowering, cone and seed production traits. *Aust. For. Res.* 1982;12:295-302.
 24. Harju A. Genetic functioning of Scots pine seed orchards. PhD thesis, University of Oulu, Finland, *Acta Universitatis Ouluensis* 271, 1995.
 25. Kang KS. Clonal and annual variation of flower production and composition of gamete gene pool in a clonal seed orchard of *Pinus densiflora*. *Can. J. For. Res.* 2000;30:1275-1280.
 26. Kang KS, El-Kassaby YA. Considerations of correlated fertility between genders on genetic diversity: *Pinus densiflora* seed orchard as a model. *Theor. Appl. Genet.* 2002;105:1183-1189.
 27. Kang KS, Kjar ED, Lindgren D. Balancing gene diversity and nut production in *Corylus avellana*. *Scand. J. For. Res.* 2003;18:118-126.
 28. Kang KS, Lindgren D, Mullin TJ. Fertility variation, genetic relatedness, and their impacts on gene diversity of seeds from a seed orchard of *Pinus thunbergii*. *Silvae Genet.* 2004;53:202-206.
 29. Kim Z, Hwang J, Lee S, Yang C, Gorovoy PG. Genetic variation of Korean pine (*Pinus koraiensis* et Zucc.) at allozyme and RAPD markers in Korea, China and Russia. *Silvae Genet.* 2005;54: 235-246.
 30. Kjær ED, Wellendorf H. Variation in flowering and reproductive success in a Danish *Picea abies* (Karst.) seed orchard. *For. Genet.* 1997;5:181-188.
 31. Lacy RC. Clarification of genetic terms and their use in the management of captive populations. *Zoo Biol.* 1995;14:565-577.
 32. Lindgren D, El-Kassaby YA. Genetic consequences of combining selective cone harvesting and genetic thinning in clonal seed orchards. *Silvae Genet.* 1989;38:65-70.
 33. Lindgren D, Mullin TJ. Relatedness and status number in seed orchard crops. *Can. J. For. Res.* 1998;28:276-283.
 34. Lindgren D, Gea LD, Jefferson PA. Loss of genetic diversity monitored by status number. *Silvae Genet.* 1996;45:52-59.
 35. Li W, Wang X, Li Y. Stability in and correlation between factors influencing genetic quality of seed lots in a seed orchard of *Pinus tabulaeformis* over a 12-year span. *PLOS ONE* 2011;6:e23544.
 36. Lynch, M. The Origins of genome architecture. Sinauer Associates,
 37. Matziris D. Variation in growth, flowering and cone production in a clonal seed orchard of Aleppo pine grown in Greece. *Silvae Genet.* 1997;46:224-228.
 38. Nei M. Analysis of gene diversity in subdivided populations. *Proc. Natl. Acad. Sci. U.S.A.* 1973;70:3321-3323.
 39. O'Reilly C, Parker WH, Barker JE. Effect of pollination period and strobili number on random mating in a clonal seed orchard of *Picea mariana*. *Silvae Genet.* 1982;31:90-94.

40. Owens JN and Fernando DD. Pollination and seed production in western white pine. *Can. J. For. Res.* 2007;37:260-275.
41. Reynolds S, El-Kassaby YA. Parental balance in a Douglas-fir seed orchard: cone vs. seed production. *Silvae Genet.* 1990;39:40-42.
42. Song J, Ratcliffe B, Kess T, Lai BS, Korecký J, El-Kassaby YA. Temporal quantification of mating system parameters in a coastal Douglas-fir seed orchard under manipulated pollination environment. *Sci. Rep.* 2018;8:11593
43. Sønstebo JH, Tollefsrud MM, Myking T, Steffenrem A, Nilsen AE, Edvardsen ØM, Johnskås OR, El-Kassaby YA. Genetic diversity of Norway spruce (*Picea abies* (L.) Karst.) seed orchard crops: Effects of number of parents, seed year, and pollen contamination. *For. Ecol. Manage.* 2018;411:132-141.
44. Wright, S. Evolution in mendelian populations. *Genetics* 1931;16:97-159.
45. Yi JS. Korean white pine (*Pinus koraiensis*). I. The Society for Korean White Pine, Kangwon, Korea. 2005;145.

Tables

Table 1 Average production of female and male strobili per ramet and correlation coefficient estimates (r) for four successive years in the 1.5-generation *P. koraiensis* clonal seed orchard

	2014	2015	2016	2017	Pooled
Female strobili	2.69	2.99	0.33	0.92	1.73
Male strobili	1.82	84.44	51.24	1912.18	512.44
r^*	-0.02	0.36	-0.14	0.09	0.22

* Person's correlation coefficient between female and male strobilus production

Table 2 Coefficient of variation for female (CV_f) and male (CV_m) strobilus production, sibling coefficient of female (y_f) and male (y_m), effective number of female ($N_p^{(f)}$) and male ($N_p^{(m)}$) parents, relative effective number of female ($N_r^{(f)}$) and male ($N_r^{(m)}$) parents, and gene diversity (GD) in the 1.5-generation *P. koraiensis* clonal seed orchard ($N = 52$)

	2014		2015		2016		2017		Pooled	
	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male
CV_f and CV_m	0.412	3.158	0.664	2.620	1.087	1.534	0.918	0.820	0.403	0.831
y_f and y_m	1.169	10.972	1.441	7.864	2.181	3.353	1.843	1.673	1.162	1.690
$N_p^{(f)}$ and $N_p^{(m)}$	44.5	4.7	36.1	6.6	23.8	15.5	28.2	31.1	44.7	30.8
$N_r^{(f)}$ and $N_r^{(m)*}$	85.5	9.1	69.4	12.7	45.9	29.8	54.2	59.8	86.0	59.2
GD	0.989	0.895	0.986	0.924	0.979	0.968	0.982	0.984	0.989	0.984

* $N_r^{(f)}$ and $N_r^{(m)}$ are relative percentages (%) to the census number (N)

Table 3. Clonal sibling coefficient (Y), parental effective number of parents (N_p), relative effective number of parents (N_r), and loss of gene diversity (GD) in the 1.5-generation *P. koraiensis* clonal seed orchard

	2014	2015	2016	2017	Pooled
Y	4.035	3.326	2.384	1.879	1.713
N_p	14.8	16.6	29.4	36.8	41.6
N_r (%)	28.4	31.9	56.6	70.8	80.0
GD loss (%)	3.4	3.0	1.7	1.4	1.2

Figures

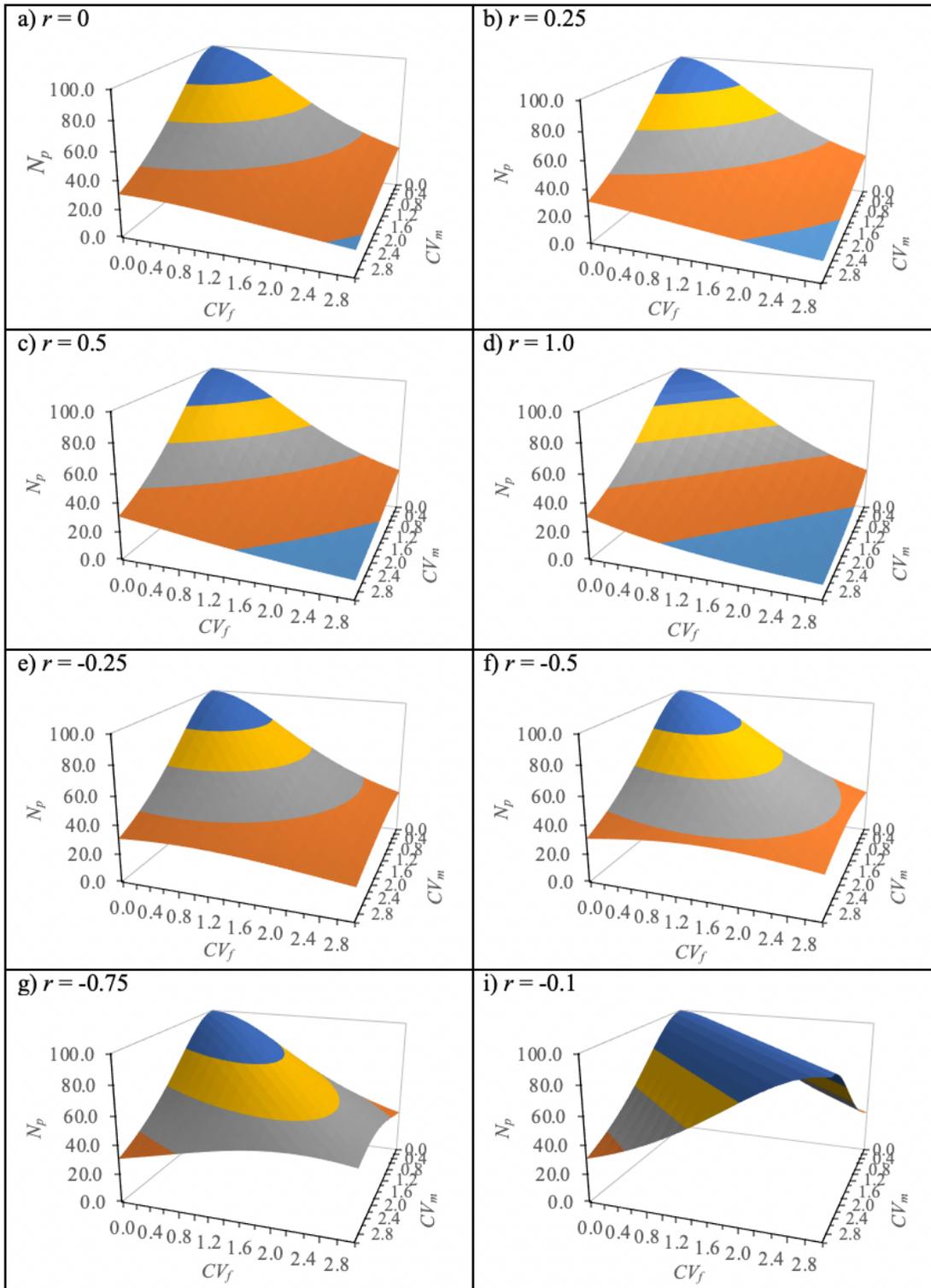


Figure 1

Stochastic simulation of the effective number of parents (N_p) with female and male fertility variation (CV_f , CV_m) under various covariation (correlation coefficients, r) between female and male reproductive outputs. The census number was set to be 100 ($N = 100$) in the population

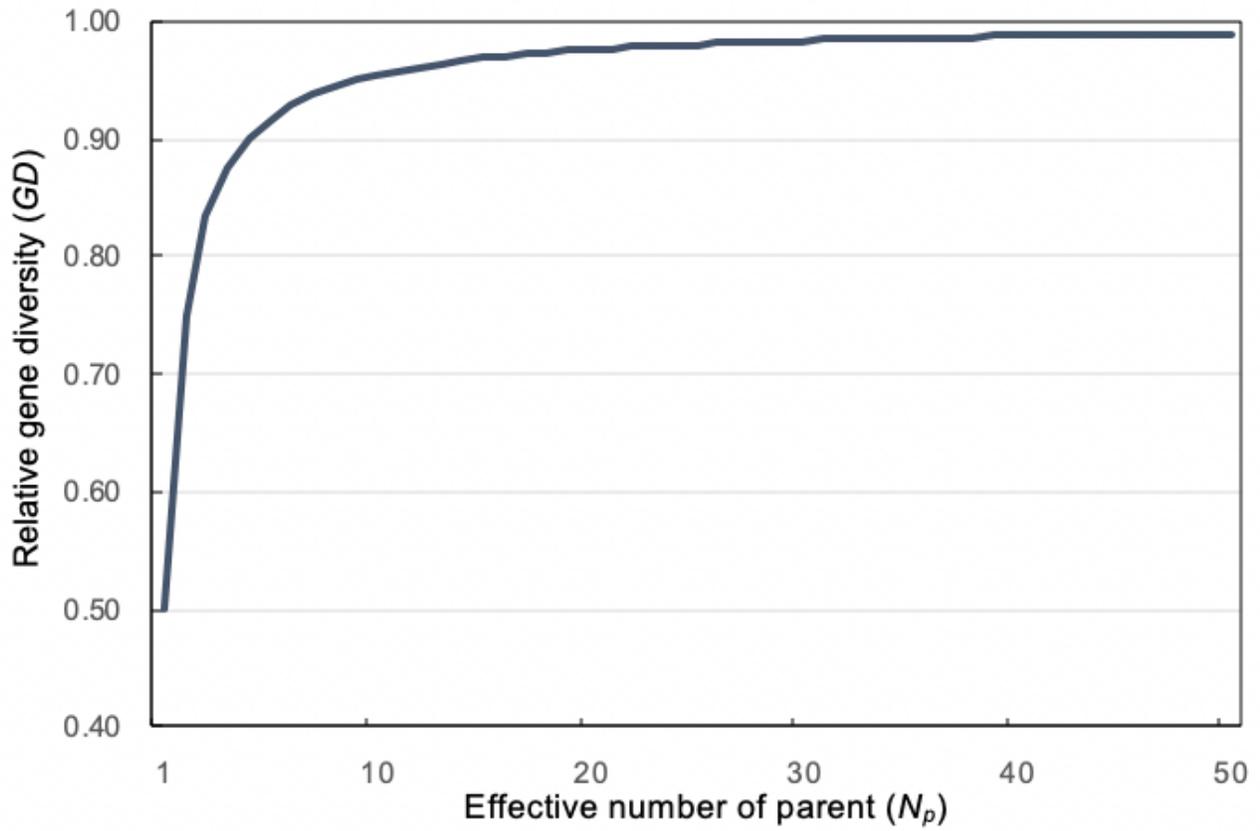


Figure 2

Relationship between seed orchard crops' effective number of parents (N_p) and gene diversity (GD) relative to their parental population

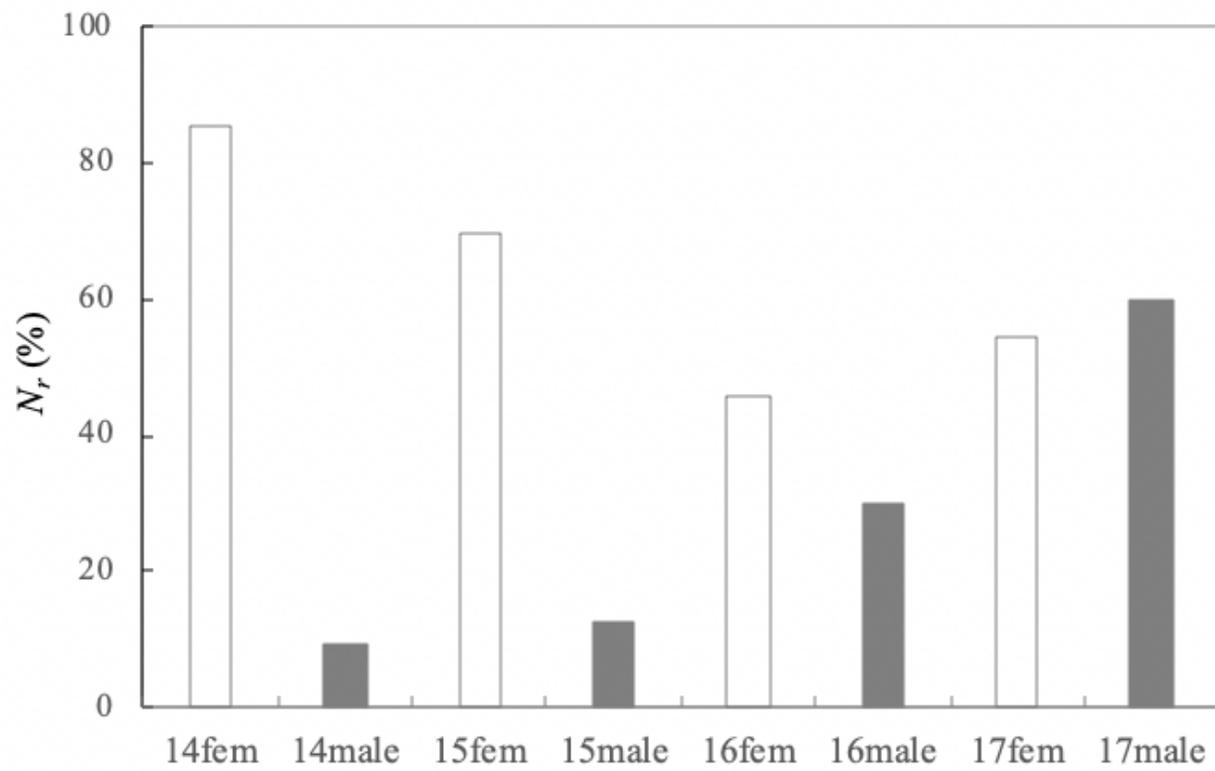


Figure 3

Relative effective number of parents (N_r , relative to census number) for female and male parents in the 1.5-generation *P. koraiensis* clonal seed orchard

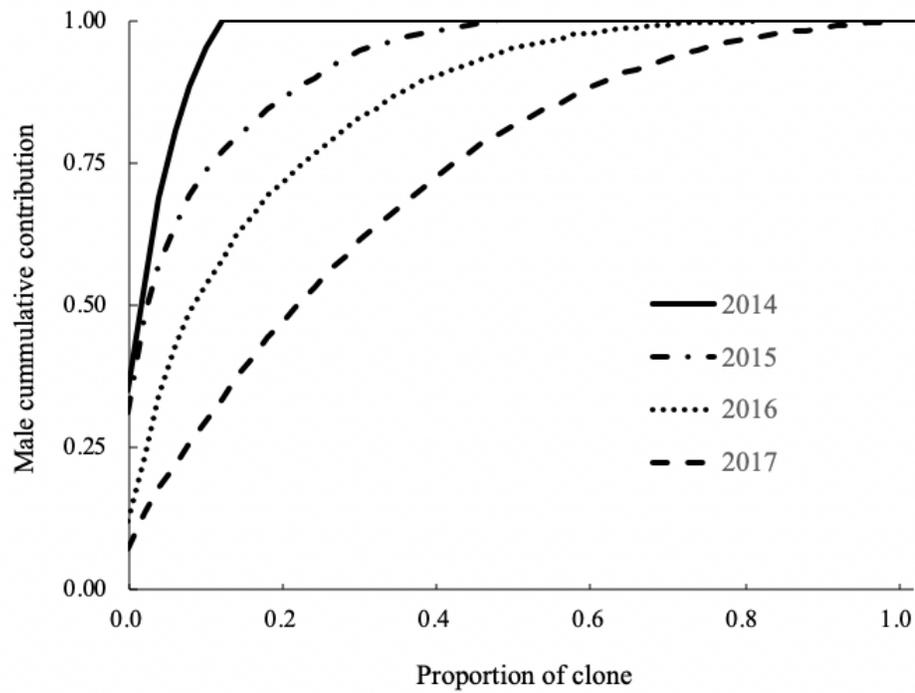
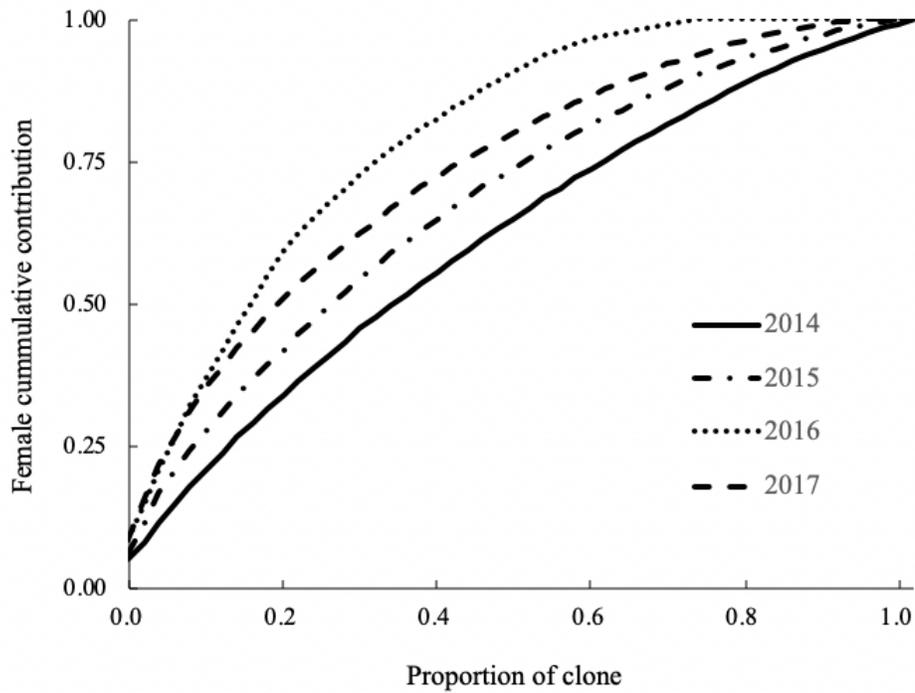


Figure 4

Cumulative contribution curves for female (upper) and male (lower) strobili production in the 1.5-generation *P. koraiensis* clonal seed orchard from 2014 to 2017

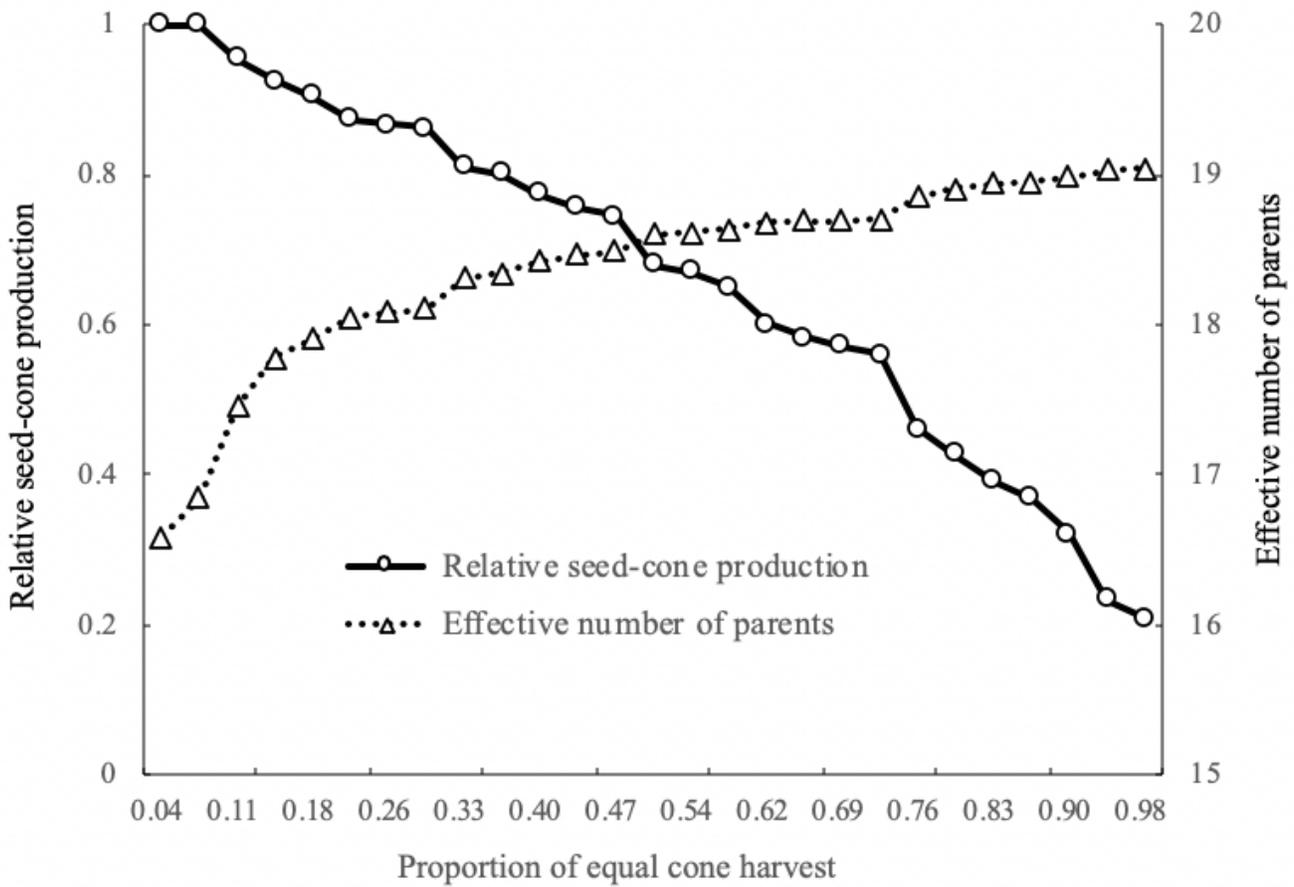


Figure 5

Trade-off between seed-cone production and effective number of parents by an equal seed-cone harvest exposed for a good crop year (2015) in the 1.5-generation seed orchard of *P. koraiensis*

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [Methods.docx](#)