

# Genetic Variation of Flower Production in Breeding Seedling Seed Orchards of *Quercus acuta* and *Q. glauca*

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## Abstract

This study was conducted to test the significant difference of fertility variation among families and to select superior families for acorn production in the breeding seedling seed orchards (BSSOs) of *Quercus acuta* and *Quercus glauca*. The seed orchards were located in Jeju island and established by seedlings raised from selected parents for genetic testing in 2006. In the spring of 2021, the numbers of female and male flower were counted from 5 to 10 individuals per family in the BSSOs. To test statistical significance of which parameter is not satisfied through the normality test, we used a nonparametric analysis. Correlation analysis was performed to quantify the association between female and male flower production. As the results, the significant difference of flower production among families was found in both seed orchards. The averages of female flower production were 65.3 and 181.9 in *Q. acuta* and *Q. glauca*. The positive Spearman's rank correlation was existed between male and female flower production. Broad-sense heritability on female and male flower production were 0.191 and 0.147 in *Q. acuta*, and 0.285 and 0.068 in *Q. glauca*, respectively. Sexual asymmetry (e.g., maleness index) between female and male, and contribution variation among families (e.g., parental balance) were analyzed to find reasonable alternatives in the management of seed orchards. Effective population size of seed crops was predicted as a concept of status number. Loss of gene diversity (accumulation of group coancestry) would not be alarming in the BSSOs. Our results would be helpful to select breeding materials for establishing new seed orchards and to supply genetically improved seeds of evergreen oaks, which is one of the backbones of the strategy of carbon sink in the 2050 Carbon Neutrality of Korea Forest Service.

**Key Words:** breeding seedling seed orchard, fertility variation, nonparametric statistics, sexual asymmetry

## Introduction

Starting with the Climate Change Convention adopted in Rio in 1992, the Kyoto Protocol in 1997 and the Paris Climate Agreement in 2015, international interest in climate changes continues to grow. In January 2021, when the

application of the Paris Climate Agreement began, the Korea Forest Service announced its "Strategy of Forest Sector to Achieve 2050 Carbon Neutrality". The Korea Forest Service plans to plant 3 billion trees over the next 30 years to contribute to carbon neutrality. Therefore, it is necessary to strengthen the carbon absorption capacity of for-

Received: November 5, 2021. Revised: February 5, 2022. Accepted: March 15, 2022.

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ests while expanding forests that are strong against climate crisis. In particular, the need for artificial planting of warm temperate species has emerged to cope with rising temperatures caused by global warming. One of the tree species is evergreen oaks that show excellent carbon absorption capacity and environmental adaptability.

Among the evergreen oaks, *Quercus acuta* has high carbon-absorbing functions and high value as wood because its wood is heavy, conservative and does not break easily (Korea Forest Service 2021). In addition, it is expected to serve as tide-water control forest and street tree in warm temperate regions due to its sound resistance, strong composition, pollution resistance, and fire resistance. On the other hand, *Quercus glauca* has high tolerance with salinity and tidewater, making it suitable for coastal landscaping and for street tree because it is resistant to pollution. It is also utilized as wood, and is expected to be developed into bonsai, park tree, and garden tree with its beautiful leaves (KNA 2016b).

The flowering and genetic characteristics of *Q. acuta* and *Q. glauca* are featured that individual flowers are either male or female, and both sexes can be found on the same plant (monoecious). They are pollinated by wind, and flower on May and produce acorn in October of the following year. It takes two years from flowering to fruiting in *Q. acuta*, on the other hand, it takes one year from blooming to acorn production in *Q. glauca* (Chang et al. 2011; KNA 2016a, 2016b). *Q. acuta* has a very strong sprouting ability, so it is possible to renew the sprouting, and some in the natural group form a clone structure. *Q. glauca* has some shade tolerant as a semi-shade-tolerance tree, so it grows well in shade or dry land, and transplantation is relatively easy.

The ecological and physiological characteristics of the *Q. acuta* and *Q. glauca* are as follows. *Q. acuta* is distributed in the Northeast Asian region, including Korea and Japan. In Korea, it is mainly distributed in Jeju Island and coastal areas of Jeollanam-do (Lee and Choi 2010). *Q. acuta* is an evergreen broad-leaved tree with a height of 20 m and a diameter of 60 cm (Seoul National University Forests 2012). *Q. glauca* is distributed in the Himalayas, Vietnam, Japan, and Taiwan. It is mainly distributed on the southern coast and Jeju Island in Korea. It is an evergreen tree with a height of 15 m (Chang et al. 2011).

This study attempts 1) to test the statistical significance on the difference of flower production among families in the seedling seed orchards of *Q. acuta* and *Q. glauca* established at Seogwipo-si, Jeju island, 2) to estimate the gene diversity of seeds and the heritability of flowering characteristics based on the analysis of variance (ANOVA), and 3) to evaluate Spearman's rank correlation between female and male flower production. Our results would contribute to select and utilize superior families and/or individuals in the establishment of the advanced generation seed orchards of evergreen oaks. In addition, this study could also support "2050 Carbon Neutrality" policy of the Korea Forest Service (Korea Forest Service 2021).

## Materials and Methods

### *Seed orchards and flowering survey*

Breeding seedling seed orchard (BSSO) is a seed orchard that can be acting both genetic testing and seed production at the same time. Each family of the BSSO refers to seedlings raised from the seed of plus tree selected. In both *Q. acuta* and *Q. glauca*, plus trees were selected from various sites in Jeju island, seeds were then collected from the plus trees. Seedlings were produced and used to create the BSSOs with a design of row tree-plot.

The BSSOs of *Q. acuta* and *Q. glauca* were formed with half-sib families at the size of 2.0 ha in 2006, respectively. They are located at 33°18'N, 126°33'E and altitude 700 m at Sanghyo-dong, Seogwipo-si, Jeju-do. The BSSO of *Q. acuta* composed of 41 families and 1,312 trees, and that of *Q. glauca* composed of 36 families and 621 individuals. Among the composition, a total of 41 families and 202 individuals were investigated in *Q. acuta*. and 28 families and 242 trees were surveyed flower production in *Q. glauca*.

Abundances of male and female flower were surveyed in the BSSOs of *Q. acuta* and *Q. glauca* in May 2021. Numbers of female and male flower were counted from 5 to 10 individuals per family in the BSSOs, considering sample representatives. The male flower of *Q. acuta* and *Q. glauca* are characterized by a stretched form of ament, which is a characteristic of the oak genus, and the discovery rate is high. The female flower of *Q. acuta* and *Q. glauca* is in axilla of the leaf. For the difficulty of counting the small flowers, the numbers of female flowers were estimated by multi-

plying the average number of flowers per branch bearing flowers by a percentage of flowering area in the whole area of crown. The numbers of male flowers were estimated by multiplying the average number of flowers per branch by the total number of branches bearing flowers. For statistical analysis, the numbers of female and male flowers were standardized by subtracting the average and dividing it by the standard deviation. (Na et al. 2014).

### Statistical analysis and heritability estimation

The data of male and female flowers were converted into variables using  $\log_{10}(1 + \text{counting})$  in order to improve accuracy (Steel and Torrie 1980; Han et al. 2001). One-way ANOVA was conducted as a method of analyzing the variances of male and female flowers among families, which analyze whether there was a significant difference in the flowering characteristics among families. The hypotheses were set as the null hypothesis ' $H_0$ : The flower production among families is the same' and the alternative hypothesis ' $H_1$ : The flower production is not same among families', and then the normality and homoscedasticity of the flower data were tested.

In this study, the broad-sense heritability was derived using the results of variance analysis of the male and female flower production of *Q. acuta* and *Q. glauca*. A broad-sense heritability ( $H^2$ ) is defined as follows (Wray and Visscher 2008).

$$H^2 = \frac{V_G}{V_P} = \frac{V_G}{V_G + V_E} = \frac{\sigma_f^2}{\sigma_f^2 + \sigma_e^2}$$

In the formula, the genetic variance ( $V_G$ ) was obtained by the variance among families. The phenotypical variance ( $V_P$ ) is the sum of environmental variance and genetic variance, and environmental variance ( $V_E$ ) is calculated as the value of error variance which equates to the variance within families. Therefore, the heritability could be estimated using the variance of family ( $\sigma_f^2$ ) and the variance of error ( $\sigma_e^2$ ).

Spearman's rank correlation was conducted to investigate the correlation between the amount of male and female flowers. Prior to conducting the correlation analysis, the null hypothesis ' $H_0$ : The female and male flower production are correlated each other' and the alternative hy-

pothesis ' $H_1$ : The female and male flowers are not correlated' were established. The hypotheses were verified through the p-value of the correlation analysis. R for window version 4.05 was used for ANOVA and correlation analysis (R Core Team 2019).

### Maleness index and parental balance curve

Based on the variable-transformed data of female and male flower production, the maleness index ( $A_i$ ), sexual unbalancing, was calculated as shown in the formula below (Lloyd 1979).

$$A_i = \frac{m_i}{f_i + m_i}$$

where  $f_i$  and  $m_i$  are the relative proportion (contribution) of the female and male flower production of the  $i$ -th family on the total flower production.

The contribution of each family to how uniformly contributing was analyzed based on a parental balance curve. The parental balance curve was drawn as families sorted in descending order were on the  $x$ -axis, and the accumulated contribution of each family to the total flower production was on the  $y$ -axis. This cumulative contribution curve is an important for improving the expectations for equal contribution of families in creating the seed orchard and managing plan of it in the future.

### Status number and gene diversity

Gene diversity of the seed crops was estimated by the status number which was calculated by the group co-ancestry ( $\Theta$ ) (Na et al. 2014). The group co-ancestry refers to the possibility of incest-breeding, which is predicted to occur in the next generation when spouse-breeding is randomly performed (Cockerham 1967; Lindgren and Mullin 1998).

In breeding seedling seed orchards such as *Q. acuta* and *Q. glauca* seed orchards, it is assumed that there is half-sib relationship among individuals within a family. The self co-ancestry of individual itself is 0.5, so the group co-ancestry could be estimated as follows (Kang et al. 2001; David et al. 2003; Na et al. 2014).

$$\Theta = \frac{0.5 \sum_{i=1}^N n_i + 0.125 \sum_{i=1}^N (n_i^2 - n)}{n^2}$$

where  $\Theta$  is the group co-ancestry,  $N$  is the total number of families,  $n$  is the total number of individuals and  $n_i$  is the individual number of the  $i$ -th family.

Status number ( $N_s$ ) is defined as half of the reciprocal of the group co-ancestry. Therefore,  $N_s$  is calculated as follows (Lindgren and Mullin 1997; Kang et al. 2005).

$$N_s = \frac{1}{2\Theta} = \frac{0.5n^2}{0.5 \sum_{i=1}^N n_i + 0.125 \sum_{i=1}^N (n_i^2 - n_i)}$$

$$= \frac{n^2}{\sum_{i=1}^N n_i + 0.25 \sum_{i=1}^N (n_i^2 - n_i)}$$

Relative status number ( $N_r$ ) is obtained from dividing the status number by the total number of individuals (Kang and Lindgren 1998) and calculated as follows as  $N_r = N_s/n$ .

Gene diversity ( $GD$ ) was estimated using the concept of the status number that is directly connected to the group co-ancestry. The gene diversity of seed orchard crop refers to the expected heterozygosity of the founder parents, and the  $GD$  was estimated as follows (Nei 1973; Kang and Lindgren 1998).

$$GD = 1 - \frac{1}{2N_s} = 1 - \Theta$$

## Results and Discussion

### Female and male flower production

The production of female and male flower of *Q. acuta*

**Table 1.** Female and male flower production in breeding seedling seed orchards of *Q. acuta* and *Q. glauca*

Character	<i>Q. acuta</i>		<i>Q. glauca</i>	
	Female	Male	Female	Male
Total individual ( $N$ )	202	202	242	242
Mean	65.3	2,799.5	181.9	16.6
Coefficient of variation ( $CV$ )	0.46	0.34	0.61	0.16

and *Q. glauca* is shown in Table 1. The total individual of *Q. acuta* was 202 trees, and the average of female flowers was 65.3 and the average of male flowers was 2,799.5 (Table 1). The standard deviation of the number of female flowers was 143.05, and that of the male was 8140.08. In the case of the coefficient of variation, the  $CV$ s of female and male flower production were 0.46 and 0.34, respectively. This result implies that the variation of female flower production among families is slightly larger than that of males (Table 1).

The total number of 242 trees was surveyed for female and male flower production in the seed orchard of *Q. glauca*. The average of female flower was 181.9, and that of male was 16.6 (Table 1). The standard deviations of female and male flower production were 297.9 and 102.6, respectively. In the case of the coefficient of variation, female and male flower production were 0.61 and 0.16, indicating that the variation in the number of female flower production among families was greater than that of male flower (Table 1).

### Analysis of variance and estimation of heritability

As a result of testing the normality of female and male flower production through the Shapiro-Wilk normality test, the p-value of female flower production was calculated as 1.213e-15, and that of male flower production was calculated as 4.797e-13 in *Q. acuta*. Both male and female p-values were found to be less than the significance level of 0.05, so they were not normal. The modified robust Brown-Forsythe Levene-type test showed that the production of male and female flower had homoscedasticity in *Q. acuta*. In the same method, the normality of female and male flower production was not found in *Q. glauca*, and also male and female flowers were not recognized for their homoskedasticity.

For analyzing the variance of nonparametric data, the Kruskal-Wallis rank sum test was conducted on the conversion data of male and female flower production in *Q. acuta*. As a result, the null hypothesis is rejected because the p-value of *Q. acuta* female flower production was 0.002 and that of the male was 0.015, which are less than the significance level of 0.05. Therefore, it was judged that there was a significant difference in the female and male flower production among families by adopting the alternative hypothesis ' $H_1$ : The flower production is not same among

families'.

As a result of the Kruskal-Wallis rank sum test of *Q. glauca*, the null hypothesis was rejected because the p-value of female flower production was 1.703e-06, which is less than the significance level of 0.05. Therefore, the alternative hypothesis 'H<sub>1</sub>: The flower production is not same among families' was adopted. But, the p-value of male flower production was 0.161, and thus the null hypothesis cannot be rejected. It was concluded that there was a significant difference in the production of female flower, but no significant difference in the production of male flower among families in the breeding seedling seed orchard of *Q. glauca*.

The one-way ANOVA showed that the difference of female and male flower production among families was significant at the significance level of 0.05 in the breeding seedling seed orchards of *Q. acuta* and *Q. glauca* (Table 2). Variance components and heritability estimates for production of female and male flowers are presented in Table 2. The broad sense heritabilities of female and male flower were 0.641 and 0.684 in *Q. acuta*. On the other hand, the broad-sense heritability of male (0.704) was much higher than that of female (0.589) in *Q. glauca*. This result is implying that female and male flower production are under strong genetic control (Han et al. 1985; Kang et al. 2005).

Heritability is the degree to which the traits of parents are transmitted to their offspring. It varies depending on individuals and sites, so both genetic and environmental influences should be considered altogether. There are broad-sense heritability and narrow-sense heritability. The former is the ratio of all genetic variance to phenotypic variance, and the latter is the ratio of additive genetic variance to phenotypic variance (Han et al. 1985). Therefore, the nar-

row-sense heritability indicates exact direction on a specific gene rather than the broad-sense heritability.

Spearman's rank correlation analysis was conducted to find out the change of rank between female and male flower production. As a result, the p-value of the production of flower of *Q. acuta* that underwent variable conversion was 1.609e-08, which was less than the significance level of 0.05. In addition, the rank correlation coefficient was 0.389, indicating that there was a positive relation on the flower production between female and male in *Q. acuta*. The covariance was 1,195.6 (Table 3).

Similarly, the p-value of the amount of female and male flowers of *Q. glauca* was less than the significance level of 0.05. The correlation coefficient and the covariance were also positive between female and male flower blooming (Table 3). This information would be expected to support the establishment strategy of seed orchard using selected individuals or families with good flower production.

#### *Maleness index and parental cumulative curve*

The maleness index of *Q. acuta* families showed a great deviation from the expectation of sexual balance (Fig. 1).

**Table 3.** Spearman's rank correlation coefficient between female and male flower production in breeding seedling seed orchards of *Q. acuta* and *Q. glauca*

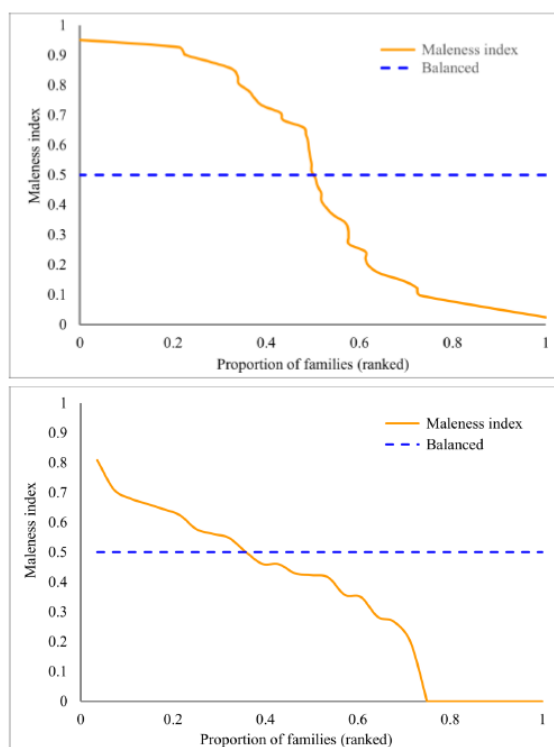
Character	<i>Q. acuta</i>	<i>Q. glauca</i>
Correlation coefficient ( <i>r</i> )	0.389***	0.229***
p-value	1.61e-08	0.0003
Covariance	1,195.6	656.1

\*\*\*p < 0.001.

**Table 2.** Analysis of variance ( $\sigma_f^2$  and  $\sigma_e^2$ ) and broad-sense heritability ( $H^2$ ) estimates for female and male flower production in the seed orchards of *Q. acuta* and *Q. glauca*

Character	<i>Q. acuta</i>		<i>Q. glauca</i>	
	Female	Male	Female	Male
Variance of family ( $\sigma_f^2$ )	1.710	3.999	2.333	0.522
Variance of error ( $\sigma_e^2$ )	0.957	1.850	1.627	0.220
F-value	2.184***	1.862**	3.304***	1.731**
Heritability ( $H^2$ )	0.641	0.684	0.589	0.704

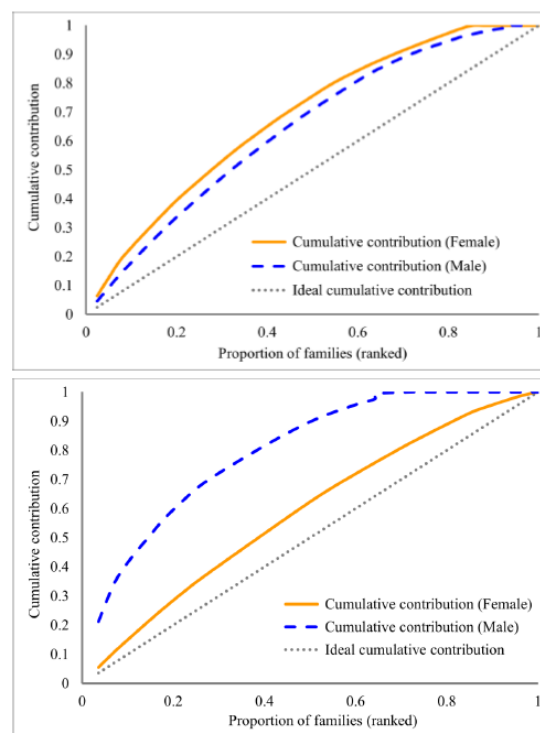
\*\*\*p < 0.001, \*\*p < 0.01, \*p < 0.05.



**Fig. 1.** Maleness index by proportion of families in breeding seedling seed orchards of *Q. acuta* (upper) and *Q. glauca* (lower). Horizontal line indicates the complete balance of flower production between female and male.

As shown in Fig. 1, the dotted horizontal line shows the complete gender balance between female and male contribution. Compared to *Q. acuta*, the maleness index of *Q. glauca* was located more closely to the expectation line, meaning that families of *Q. glauca* are more balanced in gamete production between female and male. However, it should be said that the maleness index deviated a lot from the expectation of 0.5 (horizontal dotted line) in the seedling seed orchards of *Q. acuta* and *Q. glauca*.

The maleness index gave an information on the situation of sexual imbalance between female and male flower production. It could be said that the *Q. acuta* are closer to the sexual balance than the *Q. glauca*. It will be expected to find out more accurate situation of imbalance between acorn and pollen production by the maleness index for several years. The gametic contribution to flower production between genders was not under expectation (i.e., balanced) in breeding seedling seed orchards of *Q. acuta* and *Q. glauca* (Fig. 1).



**Fig. 2.** Cumulative contribution curve to flower production by proportion of families ranked in breeding seedling seed orchards of *Q. acuta* (upper) and *Q. glauca* (lower). The dotted diagonal line means an equal contribution among families.

If the maleness index ( $A_i$ ) is 1, the individual contributes 100% as a male parent and does not produce any female flower. If the  $A_i$  equals 0, then the individual does not produce any male flowers and contributes as only female parents. For both cases, it is said that they are under complete sexual imbalance (Lloyd 1979; Han et al. 2001; Kim et al. 2008). Under sexual balancing, all individuals or families should be equally contributing (i.e.,  $1/N$ ) to the production of female and male flower production. However, it is hardly fulfilled in any real condition of seed orchards (Kang et al. 2005; Na et al. 2014).

Variation of parental contribution among families could be described as the parental cumulative curve as shown in Fig. 2. When there is equal production of flower production among families, the cumulative contribution curve is linear as the dotted diagonal line in the Fig. 2. However, the cumulative contribution of both species was far from the expectation of equal contribution (Fig. 2). Only a few families were highly contributing to produce female and male

gametes.

In the breeding seedling seed orchard of *Q. acuta*, the female parental balance curve was slightly more far from the idea (equal) contribution, compared to male parents. On the other hand, the female cumulative curve was relatively closer to the ideal cumulative contribution than males in the *Q. glauca* seed orchard. In other words, *Q. acuta* shows lower variation in the production of male flower than that of female among families, while *Q. glauca* has lower variation of female than male production among families (Kim et al. 2020).

In the BSSO of *Q. acuta*, the top 20% fertile families accounted for 39% and 33% of female and male flower production. Similarly, the top 20% productive families were contributing 30% and 61% to female and male flower production in the BSSO of *Q. glauca* seed (Fig. 2). Thus, the most productive families could be considered when the superior families are selected for acorn production and genetic thinning.

#### Estimation of status number and gene diversity

The  $N_s$  of *Q. acuta* seed orchard was higher (101.3) than that (78.3) in *Q. glauca* seed orchard, and the  $N_r$  of *Q. acuta* seed orchard is 0.50, and that of *Q. glauca* is 0.32 (Table 4). This result explains that only 50% and 32% of the individual of the seed orchards are equally contributing to the production of flowers, that is, seed production. Thus, some managerial options, such as promoting flowering and/or fertilization should be considered for producing genetically superior quality seeds from the breeding seedling seed orchards.

The group co-ancestry in the *Q. acuta* and *Q. glauca* seed orchards were calculated as 0.0049 and 0.0064, respectively. The gene diversity was estimated to be 0.995

and 0.994, respectively (Table 4). Therefore, it was possible to estimate 4.9% loss of gene diversity in the *Q. acuta* seed orchard and 6.4% decrease in the *Q. glauca* seed orchard compared to the orchard parents (i.e., founder population).

The status number ( $N_s$ ), relative status number ( $N_r$ ), group co-ancestry ( $\Theta$ ), and gene diversity ( $GD$ ) were calculated using the number of trees in each family (see M & M). The status number is linked with group co-ancestry, which describes accumulation of inbreeding and loss of gene diversity in the orchard seeds (Cockerham 1967; Lindgren and Mullin 1997, 1998). The status number (i.e., effective population size) based on the variation of flower production is one of the important estimators in the seed orchard management. In seed orchards, it is crucial to maintain gene diversity as individuals are often related or hybrid.

In order to select good quality genetic materials (plus-trees or families), growth characteristics such as height, diameter and volume must be investigated along with the amount of seed production. This study was conducted with the aim of expanding the afforestation of warm-evergreen species with excellent carbon absorption capacity and preparing for global warming in accordance with the Korea Forest Service's Strategy to achieve 2050 Carbon Neutrality. Therefore, the amount of acorn production and carbon absorption capacity should also be considered in order to expand the afforestation of *Q. acuta* and *Q. glauca*.

*Q. glauca* blooms in May and forms seeds in October of that year. However, *Q. acuta* takes two years from flowering to acorn production, meaning that it cycles every two years to understand the relationship between flowering and fruiting in *Q. acuta*. Therefore, it seems that research for at least two years is needed to select the best plus trees or families for establishment new seed orchards of *Q. acuta*.

## Acknowledgements

This study was carried out with the support of 'R&D Program for Forest Science Technology (Project No. 2022458B10-2224-0201)' provided by Korea Forest Service (Korea Forestry Promotion Institute).

**Table 4.** Status number ( $N_s$ ), relative status number ( $N_r$ ), group co-ancestry ( $\Theta$ ), and gene diversity ( $GD$ ) of seeds in breeding seedling seed orchards of *Q. acuta* and *Q. glauca*

Estimator	<i>Q. acuta</i>	<i>Q. glauca</i>
Status number ( $N_s$ )	101.3	78.3
Relative status number ( $N_r$ )	0.50	0.32
Group co-ancestry ( $\Theta$ )	0.0049	0.0064
Gene diversity ( $GD$ )	0.995	0.994

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