

EFFECTIVE SIZE OF AUTO-TETRAPLOID POPULATION UNDER PARTIAL SELFING

Ukuran Efektif Populasi Autotetraploid yang Secara Parsial Menyerbuk Sendiri

Muhamad Sabran

*Indonesian Center for Agricultural Biotechnology and Genetics Resources Research and Development
Jalan Tentara Pelajar 3A, Kampus Penelitian Pertanian Cimanggu, Bogor 1611
Telp. (0251) 8337975 Fax. (0251) 8338820
Email:msbran23@yahoo.com*

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ABSTRAK

Ukuran efektif suatu populasi adalah banyaknya individu dalam populasi ideal yang memiliki jumlah dispersi frekuensi alel akibat penumpukan genetik atau proporsi perkawinan antar kerabat yang sama dengan populasi tersebut. Ukuran efektif populasi dipengaruhi oleh banyaknya individu dalam populasi dan sistem perkawinan antar individu. Pada populasi autotetraploid, ukuran efektif populasi juga dipengaruhi oleh peluang terjadinya reduksi ganda, adalah suatu peristiwa meiotik ketika dua kromatid yang berasal pembelahan induk kromatid yang sama bergabung kembali membentuk gamet. Penelitian ini bertujuan untuk mempelajari pengaruh reduksi ganda dan peluang terjadinya penyerbukan/perkawinan sendiri pada populasi yang dapat kawin secara acak, tapi dapat juga kawin/menyerbuk sendiri terhadap ukuran efektif populasi. Rumus untuk ukuran populasi efektif diturunkan dengan menyamakan nilai ragam perubahan frekuensi gen pada populasi ideal dengan nilai ragam tersebut pada populasi yang memiliki sembarang peluang menyerbuk sendiri dan reduksi ganda. Rumus yang dihasilkan dan kajian numerik berdasarkan rumus tersebut menunjukkan bahwa ukuran efektif populasi menurun dengan meningkatnya peluang reduksi ganda dan peluang menyerbuk sendiri. Bila penyerbukan sendiri terjadi secara lengkap, maka ukuran efektif populasi tidak dipengaruhi oleh peluang reduksi ganda.

Kata kunci: ukuran efektif, autotetraploid, parsial selfing

ABSTRACT

Effective population size is defined as the number of breeding individual in an idealized population that would show the same amount of dispersion of allele frequencies under random genetic drift or the same amount of inbreeding as the population under consideration. Effective population size depends on the census size of the population and the mating system. In autotetraploid population, effective population size also depends on the probability of double reduction, i.e., a meiotic event when two sister chromatids end in the same gamete. In this research, we will study the effect of the probability of double reduction on the effective size of autotetraploid population reproduced by partial selfing. The formula for the effective population size was derived by equating the variance of the change in gene frequency in idealized population and its value in the autotetraploid population with arbitrary rate of partial selfing and double reduction. The resulted formula, and numerical study based on the formula, indicated that the effective size decreases by the increase of probability of double reduction and the rate of selfing. When there is complete selfing, however, the effective size is not affected by the probability of double reduction.

Key words: effective size, auto-tetraploid, partial selfing

INTRODUCTION

Polyploidy species are commonly classified in two major types according to their formation, i.e., allopolyploid as the result of hybridization between different taxa and subsequent chromosome doubling, and autopolyploid which stem from the chromosome doubling of the same genome primarily by fusion of unreduced gametes (Bever and Felber, 1992; Bregtagnolle and Thomson, 1995). Autotetraploidy was thought to be rare and maladaptive as compared to allopolyploidy. However, a growing number of studies using genetic information in addition to cytological and morphological traits confirm that autotetraploidy are common and of greater evolutionary and breeding importance than originally thought (Riesberg and Doyle, 1989; Soltis and Soltis, 1989; Holliste *et al.*, 2012; Dar *et al.*, 2012; Wu *et al.*, 2013). Some examples of naturally autotetraploid crops are potatoe, alfalfa, wheat, cotton, apple and peanut.

A unique aspect of autopolyploid genetics is double reduction, i.e., two sister chromatids can end in the same gamete as a result of homologous chromosomes forming a quadrivalent, followed by crossing over between the locus and spindle attachment. The probability of this meiotic event is defined as the coefficient of double reduction. Double reduction is the major biological cause of segregation distortion in autotetrasomic linkage analysis, and the coefficient of double reduction at any locus depends to a great extent on its genetic distance from the centromere (Bailey, 1961). It also plays a dominant role in evolution of autotetraploid genomes (Brutruile and Boiteux, 2000). Bailey (1961) pointed out that no theoretical basis exists for predicting the frequency of any given mode of gamete formation in terms of the recombination fraction between the two loci and the two double-reduction parameters.

The phenomenon of double reduction affects the properties of population that depend on segregation. One such property is the effective population size. Effective population size is defined as the number of breeding individuals in an idealized population that would show the same amount of dispersion of allele frequencies under random genetic drift or the same amount of inbreeding as the population under consideration (Wright, 1931, 1938). More generally, an effective population size may be defined as the number of individuals in an idealized population that has a value of any given population genetic quantity that is equal to the value of that quantity in the population of interest (Crow, 2010). The population genetic quantities are the one-generation increase in variance across replicate populations (variance effective population size), the one-generation change in the inbreeding coefficient (inbreeding effective population size), and the leading non-unit eigenvalue of

allele transition matrix (eigenvalue effective population size) (Sjodin *et al.*, 2005). These three effective size are closely linked, and derived from F-statistics, but they are not identical (Crow, 2010).

Various studies have been done on the variance effective size of a population based on the departure of its gene frequency from the Hardy-Weinberg equilibrium (Crow and Denniston, 1988; Caballero and Hill, 1991). The genetic frequency might be due to nonrandom mating or other causes. Pollak (1987, 1988) developed expressions of population effective size with partial inbreeding and Poisson distribution of family size, following a system of recurrent equations. Later Pollak and Sabran (1996) also develop the population effective size of polyploid population which include autotetraploid population as special case. The objective of this study, is to study the effect of the rate of selfing and probability of double reduction by deriving the variance effective size of an autotetraploid population reproduced partly by random mating and partly by selfing; with different method than that of Pollak and Sabran (1996).

THE METHOD

The method of deriving the effective size, depend on the population genetic quantity whose expression remain the same provided that we replace the census size in the idealized population with the effective size. In this study, we choose the variance of the change in gene frequency in one generation as the population genetic quantity. So, let us define an idealized population in an autotetraploid population with stable census size N as a random mating population with random chromosome segregation. The variability in the change in gene frequency in that population is solely due to random sampling of gametes which is equivalent to binomial sampling with $4N$ trials and probability of successes equal to p , the frequency of allele A . Therefore, the variance in the change of gene frequency is equal to

$$var(\delta p) = \frac{p(1-p)}{4N} \quad (1)$$

Now consider an autotetraploid population that is non-random mating and have some dispersion from the idealized population the effective size of this population is the number N_e , which satisfies

$$var(\delta p) = \frac{p(1-p)}{4N_e} \quad (2)$$

Naturally, we can obtain N_e , by first deriving the expression for $var(\delta p)$, the variance in the change in gene frequency and equate (1) and (2)

Let G be the number of successful gametes produced by randomly chosen individual in generation t . if we

number individuals in the population from 1 to N, then the possible values of G are $g_i, i=1,2,3 \dots N$, where g_i denotes the number of gametes produced by the i-th individual. The mean and variance of G is

$$E(G) = \bar{G} = \frac{1}{N} \sum_{j=1}^N g_j$$

and

$$\frac{1}{N} \sum_{j=1}^N (g_j - \bar{G})^2 \quad (3)$$

The covariance of the number of successful gametes between two randomly chosen individual is

$$\begin{aligned} cov(G, G') &= \frac{1}{N(N-1)} \sum_{j=1}^N \sum_{j'=1}^N (g_j - \bar{G})(g_{j'} - \bar{G}) \\ &= \frac{1}{N(N-1)} \left\{ \left[\sum_{j=1}^N (g_j - \bar{G}) \right]^2 - \sum_{j=1}^N (g_j - \bar{G})^2 \right\} \\ &= -\frac{1}{N(N-1)} \sum_{j=1}^N (g_j - \bar{G})^2 = -\frac{var(G)}{N-1} \quad (4) \end{aligned}$$

Since $\sum_{j=1}^N (g_j - \bar{G}) = 0$.

Please note that g_j is the number of gametes produced by the j-th individual if we know exactly which individual takes that position. Therefore g_j is fixed. However, since there are N! Possible orderings of the population, the number of gametes produced by the j-th individual, without knowing which individual takes that position, is

a random variable G_j which has the same distribution as G. Please note also that the total number of gametes produced by all individuals in the population is fixed and is equal to

$$\sum_{j=1}^N g_j = \sum_{j=1}^N G_j = NG$$

Now let p_1, p_2, p_3 and p_4 be the frequencies of individuals of type 1, 2,3 and 4. We denote individuals of type AAAA, AAAa, AAaa and Aaaa as type 1, 2, 3 and 4 respectively. The distribution of gametes produced by the four genotypes is as given in Table 1 below.

RESULTS AND DISCUSSION

Derivation of Effective Population Size

Let X_{ikji} $i=1,2,3,4; j_i = 1, 2,3, \dots, n_i, k=1,2,3$, be the number of gametes of type k produced by the j_i -th individuals of type i. Note that $X_{11j_1} = g_{j_1}$, since individual of type 1 will only produce gametes of type 1. Given that $G_{j_i} = g_{j_i}, i=1,2,3,4$; then $(X_{i1j_i}, X_{i2j_i}, X_{i3j_i})$ will be distributed according to a trinomial distribution with the number of trials equal to g_{j_i} and probability of successes equals to p_{i1}, p_{i2}, p_{i3} , where p_{ik} is the element of the i-th row and k-th column in Table 1.

The number of A alleles contributed to the next generation will be

$$\sum_{i=1}^4 \sum_{j_i=1}^{n_i} (2X_{i1j_i} + X_{i2j_i}) = 2 \sum_{j_1=1}^{n_1} G_{j_1} + \sum_{i=2}^4 \sum_{j_i=1}^{n_i} (2X_{i1j_i} + X_{i2j_i})$$

Table 1. Gametic output of autotetraploid species with probability of double reduction equal to α

Parental types	Gametic types			Divisor
	AA (type 1)	Aa (type 2)	aa (type 3)	
AAAA(type 1)	1	0	0	1
AAAa(type 2)	$2 + \alpha$	$2(1-\alpha)$	α	4
AAaa(type 3)	$1+2\alpha$	$4(1-\alpha)$	$1+2\alpha$	6
Aaaa (type 4)	A	$2(1-\alpha)$	$2+\alpha$	4

The change in the number of A alleles in one generation is

$$\begin{aligned}
 2N\bar{G} \delta p &= 2 \sum_{j_1=1}^{n_1} G_{j_1} + \sum_{i=2}^4 \sum_{j_i=1}^{n_i} (2X_{i1j_i} + X_{i2j_i}) - 2N\bar{G} (p_1 + \frac{3}{4}p_2 + \frac{1}{2}p_3 + \frac{1}{4}p_4) \\
 &= 2 \sum_{j_1=1}^{n_1} (G_{j_1} - \bar{G}) + \sum_{j_2=1}^{n_2} (2X_{21j_2} + X_{22j_2} - \frac{3}{2}\bar{G}) \\
 &\quad + \sum_{j_3=1}^{n_3} (2X_{31j_3} + X_{32j_3} - \bar{G}) + \sum_{j_4=1}^{n_4} (2X_{41j_4} + X_{42j_4} - \frac{1}{2}\bar{G}) \\
 &= 2 \sum_{j_1=1}^{n_1} (G_{j_1} - \bar{G}) + \frac{3}{2} \sum_{j_2=1}^{n_2} (G_{j_2} - \bar{G}) + \sum_{j_3=1}^{n_3} (G_{j_3} - \bar{G}) + \sum_{j_4=1}^{n_4} (G_{j_4} - \bar{G}) \\
 &\quad + \sum_{j_2=1}^{n_2} (2X_{21j_2} + X_{22j_2} - \frac{3}{2}G_{j_2}) + \sum_{j_3=1}^{n_3} (2X_{31j_3} + X_{32j_3} - G_{j_3}) \\
 &\quad + \sum_{j_4=1}^{n_4} (2X_{41j_4} + X_{42j_4} - G_{j_4}) \\
 &= D_1 + D_2 + D_3 + D_4 + C_1 + C_2 + C_3 \tag{5}
 \end{aligned}$$

Where $D_1 = 2 \sum_{j_1=1}^{n_1} (G_{j_1} - \bar{G})$; $D_2 = \sum_{j_2=1}^{n_2} (G_{j_2} - \bar{G})$; $D_3 = \sum_{j_3=1}^{n_3} (G_{j_3} - \bar{G})$; $D_4 = \sum_{j_4=1}^{n_4} (G_{j_4} - \bar{G})$; $C_1 = \sum_{j_2=1}^{n_2} (2X_{21j_2} + X_{22j_2} - \frac{3}{2}G_{j_2})$; $C_2 = \sum_{j_3=1}^{n_3} (2X_{31j_3} + X_{32j_3} - G_{j_3})$;

$$C_3 = \sum_{j_4=1}^{n_4} (2X_{41j_4} + X_{42j_4} - G_{j_4})$$

Note that,

$$\begin{aligned}
 cov(2X_{21j_2} + X_{22j_2} - \frac{3}{2}G_{j_2}, G_{j_2}) &= E [G_{j_2}(2X_{21j_2} + X_{22j_2} - \frac{3}{2}G_{j_2})] - E_{G_{j_2}} [G_{j_2} E(2X_{21j_2} + X_{22j_2} - \frac{3}{2}G_{j_2} | G_{j_2})] = 0; \\
 \text{since } E(2X_{21j_2} + X_{22j_2} - \frac{3}{2}G_{j_2} | G_{j_2}) &= 0. \text{ Hence, } cov(C_i, D_i) = 0; \text{ for } i=1, 2, 3, 4.
 \end{aligned}$$

Also,

$$Cov(2X_{21j_2} + X_{22j_2} - \frac{3}{2}G_{j_2}, 2X_{31j_3} + X_{32j_3} - G_{j_3}) = E[(2X_{21j_2} + X_{22j_2} - \frac{3}{2}G_{j_2}) E(2X_{31j_3} + X_{32j_3} - G_{j_3})] = 0$$

and hence $cov(C_1, C_2) = 0$. Similarly, it can be shown that

$$cov(C_2, D_i) = cov(C_3, D_i) = cov(C_1, C_3) = cov(C_2, C_3) = 0$$

We also have

$$\begin{aligned}
 var(C_1) &= \sum_{j_2=1}^{n_2} var(2X_{21j_2} + X_{22j_2} - \frac{3}{2}G_{j_2}) \\
 &= \sum_{j_2=1}^{n_2} \{ E_{G_{j_2}} [var(2X_{21j_2} + X_{22j_2} - \frac{3}{2}G_{j_2} | G_{j_2})] + var_{G_{j_2}} [E(2X_{21j_2} + X_{22j_2} - \frac{3}{2}G_{j_2} | G_{j_2})] \} \\
 &= \sum_{j_2=1}^{n_2} E_{G_{j_2}} [G_{j_2}(2p_{21} + p_{22})(1 - 2p_{21} - p_{22}) + 2G_{j_2}p_{21}] \\
 &= n_2 \bar{G} (\frac{1+2\alpha}{4})
 \end{aligned}$$

Since

$$\begin{aligned} \text{var}\left(2X_{21j_2} + X_{22j_2} - \frac{3}{2}G_{j_2}|G_{j_2}\right) &= G_{j_2}(2p_{21} + p_{22})(1 - 2p_{21} - p_{22}) + 2G_{j_2}p_{21} \\ &= \left(\frac{1+2\alpha}{4}\right)G_{j_2} \end{aligned}$$

and

$$E(2X_{21j_2} + X_{22j_2} - \frac{3}{2}G_{j_2}|G_{j_2}) = 0$$

Similarly, it can be shown that, $\text{var}(C_2) = n_3\bar{G}\left(\frac{1+2\alpha}{3}\right)$; $\text{var}(C_3) = n_4\bar{G}\left(\frac{1+2\alpha}{4}\right)$.

And also, $(D_1) = 4n_1V_G + 4n_1(n_1 - 1)C_{GG'}$; $\text{var}(D_2) = \frac{9}{4}n_2V_G + \frac{9}{4}n_2(n_1 - 1)C_{GG'}$;

$$\text{var}(D_3) = n_3V_G + n_3(n_3 - 1)C_{GG'}; \text{var}(D_4) = \frac{1}{4}n_4V_G + \frac{1}{4}n_4(n_4 - 1)C_{GG'};$$

$$\text{Cov}(D_1, D_2) = 3n_1n_2C_{GG'}; \text{Cov}(D_2, D_3) = \frac{3}{2}n_2n_3C_{GG'}; \text{Cov}(D_3, D_4) = \frac{1}{2}n_3n_4C_{GG'};$$

$$\text{Cov}(D_1, D_3) = 2n_1n_3C_{GG'}; \text{Cov}(D_1, D_4) = n_1n_4C_{GG'}; \text{Cov}(D_2, D_4) = \frac{3}{4}n_1n_2C_{GG'};$$

Where $V_G = \text{var}(G)$; and $C_{GG'} = \text{cov}(G, G')$ as defined in (3) and (4)

$$\begin{aligned} \text{(3) Hence, from (5), } 4N^2\bar{G}^2\text{var}(\delta p) &= \sum_{i=1}^3 \text{var}(C_i) + \sum_{i=1}^4 \text{var}(D_i) + 2\sum_{i<i'} \text{cov}(D_i, D_{i'}) = \\ \bar{G}\left[n_2\left(\frac{1+2\alpha}{4}\right) + n_3\left(\frac{1+2\alpha}{3}\right) + n_4\left(\frac{1+2\alpha}{4}\right)\right] &+ V_G\left[4n_1 + \frac{9}{4}n_2 + n_3 + \frac{1}{4}n_4\right] + C_{GG'}\left[4n_1(n_1 - 1) + \right. \\ \frac{9}{4}n_2(n_2 - 1) + n_3(n_3 - 1) + \frac{1}{4}n_4(n_4 - 1) &+ 6n_1n_2 + 3n_2n_3 + n_3n_4 + 4n_1n_3 + 2n_1n_4 \\ \left. + \frac{3}{2}n_2n_4\right]. & \end{aligned} \quad (6)$$

Substituting (4) into (6) and writing $n_i = Np_i$ for $i=1, 2, 3$ and 4 , we obtain

$$\begin{aligned} 4N^2\bar{G}^2\text{var}(\delta p) &= \bar{G}(1 + 2\alpha)N\left[\frac{p_2}{4} + \frac{p_3}{3} + \frac{p_4}{4}\right] \\ &+ \frac{N^2}{N-1}V_G\left[4p_1 + \frac{9}{4}p_2 + p_3 + \frac{1}{4}p_4 - (2p_1 + \frac{3}{2}p_2 + p_3 + \frac{1}{2}p_4)^2\right] \\ &= \bar{G}(1 + 2\alpha)N\left[\frac{p_2}{4} + \frac{p_3}{3} + \frac{p_4}{4}\right] + \frac{4N^2}{N-1}V_G\left[p(1-p) - 3\left(\frac{p_2}{16} + \frac{p_3}{12} + \frac{p_4}{16}\right)\right] \end{aligned} \quad (7)$$

Since $p = p_1 + \frac{3}{4}p_2 + \frac{1}{2}p_3 + \frac{1}{4}p_4$. It has been shown by Bennett (1968) that the genotypic equilibrium frequencies of an autotetraploid, if there are no selection satisfies the following equation:

$$p_1 = \frac{1}{6}p_3 + p + C - D; \quad p_2 = -\frac{2}{3}p_3 - 2C + D; \quad \text{and}$$

$$p_4 = -\frac{2}{3}p_3 + 2C + D$$

Where $f = \frac{\beta+2\alpha}{4-3\beta+2\alpha}$; $C = \frac{1}{4}(p_3 - p_1)$; $D = 2p(1-p)(1-f)$;

So $\frac{p_2}{16} + \frac{p_3}{12} + \frac{p_4}{16} = \frac{p_2+p_4}{16} + \frac{p_3}{12} = \frac{1}{8D} p(1-p)(1-f)$, substituting this into (7) we obtain

$$4N^2\bar{G}^2Var(\delta p) = \bar{G}_{(1+2\alpha)N}[(1-f)p(1-p)] + \frac{4N^2}{N-1}V_G \left[p(1-p) - \frac{3}{4}(1-f)p(1-p) \right]$$

$$= Np(1-p) \left[(1+2\alpha)(1-f)\bar{G} + \frac{N}{N-1}V_G(1+3f) \right] \tag{8}$$

Hence substituting (8) into (1) we obtain

$$N_e = \frac{N\bar{G}}{(1+2\alpha)(1-f) + \frac{NV_G}{(N-1)\bar{G}}(1+3f)} = \frac{N\bar{G}}{(1+2\alpha)(1-f) + \frac{S_G^2}{\bar{G}}(1+3f)} \tag{9}$$

Where $S_G^2 = \frac{N}{N-1}V_G$. For moderately large N, then $S_G^2 \doteq V_G$ and $\bar{G} = 2$. Substituting this into (9) we obtain

$$N_e = \frac{4N}{2(1+2\alpha)(1-f) + V_G(1+3f)} \tag{10}$$

Numerical Result

Based on equation (10), I made graphical presentation of the ratio of census size (N) and effective size (N_e) under various values of probability of double reduction (α) and rate of selfing (β). In Figure 1, presented the trend of the ratio as α increases for three rate of selfing, i.e., 0.1, 0.5 and 0.9, while the probability of double reduction ranges from 0.01 to 0.16. Theoretically, the probability of double

reduction could assume maximum values of 0 (with pure random chromosome segregation), 1/7 (with pure random chromatid segregation) and 1/6 (with complete equational segregation) (Butruille and Boiteux, 2000). Therefore in Figure 2, graphed the trend of the ratio as the rate of selfing increases at those three extreme value of α .

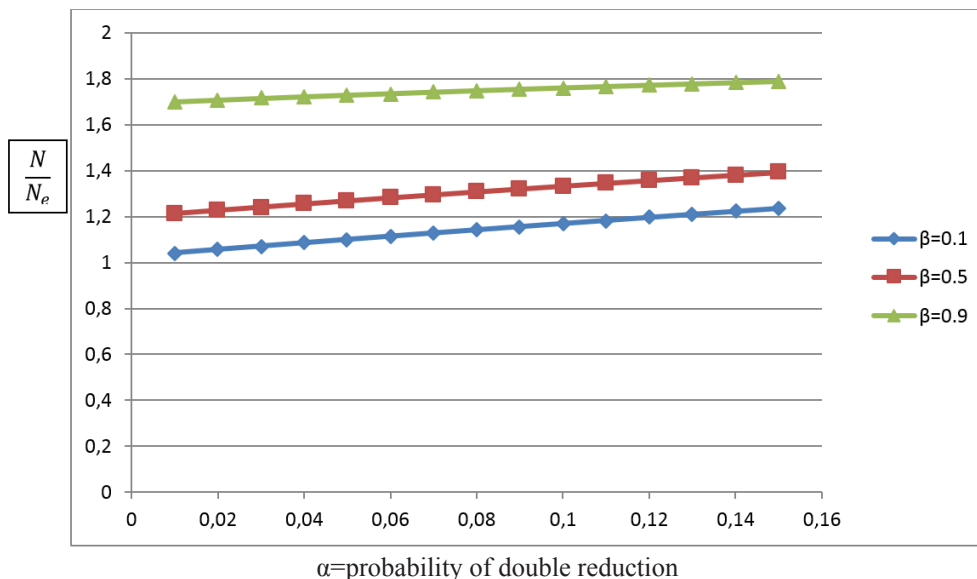


Figure 1. Ratio of census size (N) and effective size (N_e) under various values of probability of double reduction (α) and three values of the rate of selfing (β)

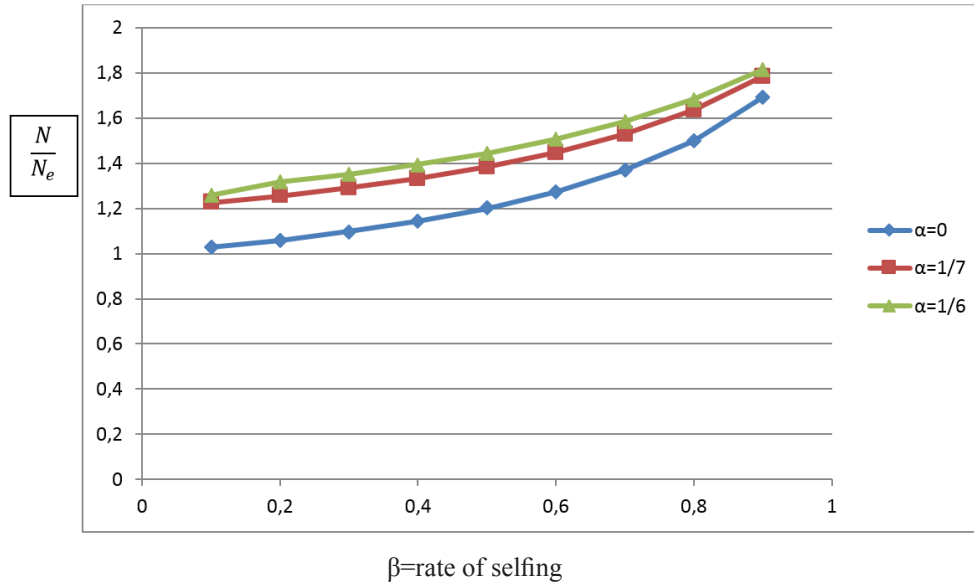


Figure 2. Ratio of census size (N) and effective size (N_e) under three values of probability of double reduction (α) and various values of the rate of selfing (β)

Discussion

Equation (10) agrees with the result obtained by Pollak and Sabran (1996). If there is random mating of gametes,

then $f=2+\alpha$, and N_e becomes

$$N_e = \frac{2N(2+\alpha)}{(1+2\alpha)(2+V_G)}$$

if in addition there is no double reduction ($\alpha=0$) and Poisson offspring distribution ($V_G=\bar{G}=2$) then $N=N_e$ as expected. When there is a complete selfing, i.e., $\beta=1$, so that $f=1$, and hence

$$N_e = \frac{N}{V_G}$$

In other words, the effective size is independent of the probability of double reduction, and its value is halve of the census size ($V_G=2$) It is also indicated in Figure 1, that when there is neither complete random mating nor complete selfing, i.e., partial selfing, the ratio $\frac{N}{N_e}$ increase linearly as the probability of double reduction increases; which means that the effective size will decrease as the probability of double reduction increase. This results was expected since both selfing and double reduction cause the departure from Hardy-Weinberg equilibrium, i.e., increase the genetic drift. Effective size of a population, describes the extent to which evolutionary change is caused by genetic drift; a lower effective size, therefore implies a greater effect of drift (Charlesworth, 2009).

Smaller populations will experience greater effects of drift relative to selection, and if a significant proportion of sites are subject to weak selection, as predicted by nearly neutral theory (Ohta, 1992), slightly deleterious mutation will be more likely to segregate at higher frequencies and fix in small populations (Akashi *et al.*, 2012). In addition, populations with small effective

size are expected to have lower probability of fixing beneficial mutations (Gossmann *et al.*, 2011, Akashi *et al.*, 2012, Gossmann *et al.*, 2012). On the other hand, double reduction cause a decrease of the equilibrium frequencies of deleterious alleles, and it has much more influence on genes subjected to gametophytic selection than on genes solely under sporophytic selection. With gametophytic selection, low frequencies of double reduction are enough to reduce equilibrium frequency severalfold (Brtruile and Boiteux, 2000)

Given the value of the probability of double reduction, the rate of selfing, and the variance of the number of successful gametes, the effective size of the population can be calculated. This effective population size can be used to determine the number of plant in an on-farm conservation or in the rejuvenation planting in order to maintain the genetic diversity or to eliminate the effect of drift in ex-situ conservation of autotetraploid population. In natural population, however, this parameter is difficult to estimate. Pedigree information might be used to estimate the effective size; however, in most natural population those information rarely available. The most widely used approach for estimating the effective size are those based genetic properties of the populations as revealed by genetic markers (Wang, 2005). The rapid development of molecular biology in recent years make it possible to obtain genetic markers and DNA sequences which can be used to extract information on effective size and other parameter of interests using appropriate statistical analysis.

CONCLUSION

The effective size decrease by the increase of probability of double reduction and the rate of selfing. When there is complete selfing, however, the effective

size does not affected by the probability of double reduction. The effect of double reduction on decreasing the effective population size does not necessarily imply that it will fix the deleterious alleles, in particular if the census size is moderately large.

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