Impacts of One-way Gene Flow on Genetic Variance Components in a Natural Population

By Xin-Sheng Hu[1*], Wen Zeng[2] and Bailian Li[2]

(Received 24th June 2002)

Abstract

Additive and dominance variances of a single adaptive quantitative trait locus (QTL) in a natural population are examined under the influence of one-way gene flow from artificial populations. The results show that the erosion of genetic variation can be substantial when gene flow takes place from genetically improved materials, characterized by a gradual increase of the alleles of interest per generation. Unlike the responses of variance components, mean fitness can increase, decrease, or remain unaltered with generation when gene flow occurs from genetically improved materials, depending upon the type of selection involved. When immigrants come from genetically unimproved materials, genetic variation is not eroded, nor is mean fitness altered. The results imply that a reduction in genetic variation in a natural forest population can occur due to immigration from genetically improved populations where the frequencies of the alleles of interest are significantly altered through different breeding designs. Attention to the erosion of genetic variation due to the ever-increasing use of genetically improved materials should be highlighted in conserving genetic resources in natural forests.

Key words: Conservation genetics, natural populations, artificial populations, gene flow.

Introduction

Conservation of natural populations is critical for the sustainable management of genetic resources or in practical genetic improvement because natural populations provide the "base" populations for creating breeding or productive populations (Zobel and Talbert, 1984). In order to meet a variety of the increasing requirements on timber products, many artificial populations, such as the intensively cultivated short-rotation plantations for industrial purposes, have been established and more will be planted in the future. Thus, it is instructive to jointly investigate the impacts of the ever-increasing use of genetically improved materials on the gene pool of natural forests, because extensive gene flow from artificial populations to natural populations has been indirectly indicated from studies on natural populations in many forest species (eg. Hamrick et al., 1993; Govindaraju, 1989). Evidences for gene flow from domesticated crops to wild relatives are also directly recorded (e.g. Ellstrand et al., 1999; Bartsch et al., 1999).

Unlike most conventional considerations where two-way gene flow among populations takes place, the one-way gene flow from artificial populations to natural populations is more important than the reverse direction gene flow when the genetic variation in natural populations is conserved. Artificial populations with genetically improved materials are often planted for purposes other than conservation. In many cases the gene flow from natural populations to artificial populations for forest timber production is ignorable; while the reverse direction of gene flow via seed and pollen dispersal could have considerable impacts on natural populations. Previously, we have often concentrated on the genetic improvement of breeding or productive populations, with an emphasis on preventing contamination of alleles from alien populations (e.g. Adams 1997). The impacts of the gene flow from genetically improved populations to natural populations are rarely stressed.

Theoretically, the significance of gene flow in homogenizing the genetic divergence among populations has long been appreciated (Wright, 1969). The role of gene flow in conservation genetics has also been extensively examined (e.g. Hamrick et al., 1993, 1994), such as in conservation of fragmented populations. However, most of these analyses are based on the results obtained using selectively neutral markers, which could provide a distinct picture of genetic variation from that obtained by studying phenotypic variation of adaptive quantitative traits (Ennos et al., 1998). Although there are many theories to account for the maintenance of quantitative trait variation (Lande, 1976; Bulmer, 1980; Barton and Turelli, 1989; Lynch, 1996), studies on the effects of gene flow on adaptive quantitative traits variation are limited (e.g. Slatkin, 1978; Cockerham and Tachida, 1987; Nagylaki, 1994; Lynch, 1994). Few reports have documented the effects of gene flow on additive and dominance components of variance for adaptive quantitative traits (e.g. Barton, 1999; Hu and Li, 2001). In addition, the gene flow in previous theoretical studies mainly refers to the two-way migration, and is not appropriate to the case where only one-way migration has a significant effect.

The purpose of this article is to examine the impacts of one-way gene flow on erosion of genetic variation in adaptive quantitative traits in natural populations, and to evaluate the potential consequences for natural forests of the increasing use of genetically improved materials. We use numerical cases to assess such impacts in terms of additive and dominance variances of a single quantitative locus (QTL). In order to gain a wide understanding of such impacts, a variety of selection types are assessed, including heterozygote advantage, heterozygote disadvantage, and frequency-dependent selection (FDS), although reports on frequency-dependent selection in tree species are limited (e.g. Ross, 1984; Richman and Kohn, 2000).

Methodology

Consider a natural population with a constant rate of immigrants of seeds and pollen grains per generation from artificial populations. The natural population size is assumed large enough so that the effect of genetic drift can be ignored. Mutation rate is assumed much smaller than that of migration rate and hence is not considered. Variance components for the environmental effects and the interaction of genotype by environment are not included.

The analysis process is based on a sequence of events in the life cycle of hermaphrodite plants: pollen flow, random combi-

[1] Department of Forestry, 3041-2424 Main Mall, University of British Columbia, Vancouver, BC V6T 1Z4, Canada

[2] Department of Forestry, North Carolina State University, P. O. Box 8002, Raleigh, NC 27695, USA

* Corresponding address (present): Xin-Sheng Hu, Department of Forestry, 3041-2424 Main Mall, University of British Columbia, Vancouver, BC V6T 1Z4, Canada.
Tel. No.: (604) 822 5609. E-mail: xhu@interchange.ubc.ca

nation of pollen grains with ovules, seed flow, natural selection, and next adults (HU and LI, 2001). Gene frequencies in migrant pollen grains or genotype frequencies in migrant seeds are assumed the same as those in the source populations at each discrete generation. For simplicity, Hardy-Weinberg equilibrium (HWE) is assumed for the genotypes in migrant seeds.

Allele frequency

Denote $p_i(t)$ and $Q_i(t)$ the frequency of allele A_i (i = 1, 2,..., n) in adults in the natural population and in artificial populations at generation t, respectively. The frequency of allele A_i in pollen grains after pollen flow, $p_{i.\mathrm{P}}(t+1)$, is given by

$$p_{i.\mathrm{P}}(t+1) = [1 - m_{i.\mathrm{P}}(t+1)]p_i(t) + m_{i.\mathrm{P}}(t+1)Q_i(t+1), \quad (1)$$

where $m_{i.\mathrm{P}}(t+1)$ is the migration rate of pollen with respect to allele A_i, and $\sum_{i=1}^{n} m_{i.\mathrm{P}}(t+1) = m_{\mathrm{tot.P}}(t+1)$, in which $m_{\mathrm{tot.P}}(t+1)$ is the total migration rate in the natural population at generation $t+1$. Thus after random combination between pollen grains and ovules, allele frequency in seeds, $p_{i.\mathrm{S}}(t+1)$, is

$$p_{i.\mathrm{S}}(t+1) = [p_{i.\mathrm{P}}(t+1) + p_i(t)]/2$$

$$= \left(1 - m_{i.\mathrm{P}}(t+1)/2\right)p_i(t) + m_{i.\mathrm{P}}(t+1)Q_i(t+1)/2. \quad (2)$$

Denote $f'_{ij}(t+1)$ the frequency of genotype A_iA_j (i, j = 1,2,..., n) after seed flow but before selection, and $f_{ij}(t+1)$ the frequency after selection at generation $t+1$. After seed flow we can show that genotype frequencies after seed flow can be expressed by

$$f'_{ii}(t+1) = \left(1 - m_{ii.\mathrm{S}}(t+1)\right)p^2_{i.\mathrm{S}}(t+1) + m_{ii.\mathrm{S}}(t+1)Q_i^{\,2}(t+1), \quad (3a)$$

$$f'_{ij}(t+1) = 2\left(1 - m_{ij.\mathrm{S}}(t+1)\right)p_{i.\mathrm{S}}(t+1)p_{j.\mathrm{S}}(t+1) + 2m_{ij.\mathrm{S}}(t+1)Q_i(t+1)Q_j(t+1), \quad (3b)$$

where $m_{ij.\mathrm{S}}(t+1)$ (i, j = 1,2,..., n) is the migration rate for genotype A_iA_j at generation t, and $\sum_{i=1}^{n}\sum_{j=1}^{n} m_{ij.\mathrm{S}}(t+1) = m_{\mathrm{tot.S}}(t+1)$, in which $m_{\mathrm{tot.S}}(t+1)$ is the total migration rate of seed at generation $t+1$. Note that genotype frequencies in the natural population do not follow HWE after seed flow.

In the two-allele case, let $m_{i.\mathrm{P}}(t) = m_{\mathrm{P}}(t)$ for A_i (i = 1,2), the same immigration rate of pollen for either A_1 or A_2, and $m_{ij.\mathrm{S}}(t) = m_{\mathrm{S}}(t)$ for A_iA_j (i, j = 1,2), the same immigration rate for each of genotype. Substituting (1) and (2) into (3a) and (3b) for the two-allele case, and ignoring the terms of the second order of migration rate, i.e. $O(m^2_{\mathrm{p}}(t+1), m_{\mathrm{S}}(t+1)\ m_{\mathrm{p}}(t+1))$, we can obtain

$$f'_{11}(t+1) = [1 - m_{\mathrm{S}}(t+1) - m_{\mathrm{P}}(t+1)]p_1^2(t)$$

$$+ m_{\mathrm{P}}(t+1)p_1(t)Q_1(t+1) + m_S(t+1)Q_1^2(t+1), \quad (4a)$$

$$f'_{12}(t+1) = 2[1 - m_{\mathrm{S}}(t+1) - m_{\mathrm{P}}(t+1)/2)p_1(t)$$

$$+ 2[m_{\mathrm{S}}(t+1) + m_{\mathrm{P}}(t+1)/2]Q_1(t+1) - 2f'_{11}(t+1), \quad (4b)$$

$$f'_{22}(t+1) = 1 + f'_{11}(t+1) - 2[1 - m_{\mathrm{S}}(t+1) - m_{\mathrm{P}}(t+1)/2]p_1(t)$$

$$- 2[m_{\mathrm{S}}(t+1) + m_{\mathrm{P}}(t+1)/2]Q_1(t+1), \quad (4c)$$

where $f'_{11}(t+1) + f'_{12}(t+1) + f'_{22}(t+1) = 1$, and $Q_1(t)$ is the frequency of allele A_1 in migrants.

Denote W_{ij} the fitness of genotype A_iA_j (i, j = 1,2,...n). After selection, genotype frequencies become

$$f_{ii}(t+1) = f'_{ii}(t+1)W_{ii}/\overline{W}(t+1), \quad (5a)$$

$$f_{ij}(t+1) = f'_{ij}(t+1)W_{ij}/\overline{W}(t+1), \quad (5b)$$

where $\overline{W}(t+1) = \sum_{i=1}^{n}\sum_{j=1}^{n} f'_{ij}(t+1)W_{ij}$. Thus, the change in gene frequency in the natural population is $\Delta p_i = p_i(t+1) - p_i(t) = f_{ii}(t+1) + \sum_{j\neq i}^{n} f_{ij}(t+1)/2 - p_i(t)$. Note that WRIGHT's (1969) formula $\Delta p_i = 0.5\, p_i(1-p_i)\, d \ln \overline{W} / dp_i$ does not hold under this case because of violation of HWE after seed flow.

Variance components

Denote the genetic values of A_iA_i and A_iA_j by a_{ij} and d_{ij}, respectively, where a and d are additive and dominance effects, respectively. The population mean after natural selection is given by $M(t+1) = \sum_{i=1}^{n} f_{ii}(t+1)a_{ii} + \sum_{1}^{n}\sum_{j\neq i}^{n} f_{ij}(t+1)d_{ij}$. For a given allele A_i (i = 1,2,...n), the conditional probability for the occurrence of genotype A_iA_j ($i \neq j$) in the natural population can be calculated according to Bayesian formula, i.e., $P_{A_iA_j/A_i}(t+1) = f_{ij}(t+1)/2p_i(t+1)$, and for genotype A_iA_i, $P_{A_iA_j/A_i}(t+1) = f_{ij}(t+1)/p_i(t+1)$. Following the method used by FALCONER (1989), the average effect of allele A_i is $\alpha_i(t+1) = p_{A_iA_j/A_i}(t+1)a_{ii} + \sum_{j\neq i}^{n} p_{A_iA_j/A_i}(t+1)d_{ij} - M(t+1)$. Thus, the variances of the additive effect, $V_A(t+1)$, and of the dominance effect, $V_D(t+1)$, are given by

$$V_{\mathrm{A}}(t+1) = 4\sum_{i=1}^{n} f_{ii}(t+1)\alpha_i^2 + \sum_{i}^{n}\sum_{j\neq i}^{n} f_{ij}(t+1)[\alpha_i(t+1) + \alpha_j(t+1)]^2, \quad (6a)$$

$$V_{\mathrm{D}}(t+1) = \sum_{i=1}^{n} f_{ii}(t+1)[a_{ii} - 2\alpha_i(t+1) - M(t+1)]^2$$

$$+ \sum_{i}^{n}\sum_{j\neq i}^{n} f_{ij}(t+1)[d_{ij} - \alpha_i(t+1) - \alpha_j(t+1) - M]^2. \quad (6b)$$

In the two-allele case, let genetic values of A_1A_1, A_1A_2 and A_2A_2 be a, d and $-a$, respectively. The variances of the additive effect, $V_A(t+1)$, and of the dominance effect, $V_D(t+1)$, can be much simplified as

$$V_{\mathrm{A}}(t+1) = 4f_{11}(t+1)\alpha_1^2(t+1) + f_{12}(t+1)(\alpha_1(t+1) + \alpha_2(t+1))^2$$

$$+ 4f_{22}(t+1)\alpha_2^2(t+1), \quad (7a)$$

$$V_{\mathrm{D}}(t+1) = [4f_{11}(t+1)f_{22}^2(t+1) + f_{12}^3(t+1) + 4f_{11}^2(t+1)f_{22}(t+1)]d^2, \quad (7b)$$

where $\alpha_1(t+1) = [(1/p(t+1) - 1)f_{11}(t+1) + f_{22}(t+1)]a + [(1/2p(t+1) - 1)]f_{12}(t+1)d$,

$\alpha_2(t+1) = -[(1/(1 - p(t+1)) - 1)f_{22}(t+1) + f_{11}(t+1)]a + [1/2(1 - p(t+1)) - 1]f_{12}(t+1)d$.

Equations (7a) and (7b) reduces to the classical results when HWE holds (see FALCONER, 1989).

Numerical cases

Two contrasting specific types of materials for artificial populations are simulated. One is the genetically unimproved material (GUM), where the frequency of allele A_1 (the two-allele case) is approximately the same as that in the natural population. The other is the genetically improved material (GIM), where the frequency of allele A_1 (the two-allele case) is gradually increased with generation due to directional selection. The first type mimics the situation where the genetic materials for artificial populations are directly sampled from the natural population, and remain so in future generation. The second type mimics the situation where materials for artificial populations are continuously genetically improved with each generation, and the replacement at each time is established with the materials with one more generation improvement than the preceding materials. It is imperative to indicate that the two types do not include all kinds of changes from different breeding strategies and genetic improvement in forest tree. The allele frequency in artificial populations may not follow the above two trends with generation in different breeding strategies, but is changed in a more complicated trend, such as the mixture of the two specific cases. Nevertheless, simulations of these two

specific cases can give insights into the impacts of gene flow from artificial populations to natural populations, and also enhance our understanding of other situations.

In the first case we set $Q_1(t)$ = 0.5 in which the frequency of allele A_1 in the initial base population is 0.5 and remains so in the future. In the second case, we assume that $Q_1(t)$ is gradually increased with generation. Note that the setting of the changing pattern in $Q_1(t)$ with generation does not affect the nature of the impacts of gene flow from artificial populations characterized by an increase in allele frequency with generation.

In the case of frequency-dependent selection, we only consider three types, although there are many definitions on the concept from different aspects (WRIGHT, 1955, 1969; see review by HEINO et al., 1998). The first type (FDS1) is that the selective advantage or disadvantage of a genotype is in proportion to frequencies of encounters with other genotypes: $W_{11} = 1+s_1(f'_{22}+f'_{12})/2$, $W_{12}=1+s_2(f'_{11}+f'_{22})/2$, and $W_{22}=1+s_3(f'_{11}+f'_{12})/2$. The second type (FDS2) is that selective advantage or disadvantage is proportional to the frequency of the genotype in question: $W_{11}=1+s_1f'_{11}$, $W_{12}=1+s_2f'_{12}$, and $W_{22}=1+s_3f'_{22}$. The last type (FDS3) is that selective advantage varies inversely with their frequencies: $W_{11}=1+s_1/f'_{11}$, $W_{12}=1+s_2/f'_{12}$, and $W_{22}=1+s_3/f'_{22}$.

Results

Simulation results indicate that gene flow from artificial populations established with GUM does not alter genetic variation in the natural population, under a variety of selection regimes. This can be viewed from (4a), (4b), and (4c) that genotype frequencies are not changed when allele frequency in migrants is the same as that in the natural population. Mean fitness and variance components remain unaltered. Thus, in the following we focus on the impacts of gene from genetically improved artificial populations.

Case I: GIM and heterozygote advantage

Let W_{11}=0.95, W_{12}=1.0, W_{22}=0.95, and a=d=1.0. If there are no effects of immigration (m_S=m_P=0), the frequency of allele A_1 eventually approaches the equilibrium level, equal to the ratio of its selection coefficient to the total selection coefficient (LI, 1976). For the given settings of fitness for each genotype, the equilibrium value of allele frequency is 0.5, and genotype frequencies are maintained at f_{11}=0.2436, f_{12}=0.5128, and f_{22}=0.2436. Homozygotes frequencies are reduced, and heterozygotes frequencies are increased, compared with their magnitudes at HWE. Additive and dominance variances are equal to V_A=0.4625 and V_D=0.2505, respectively, and mean fitness is $\bar{W}$=0.975.

When immigration from artificial populations takes place, say m_S=0.05 and m_P=0.10, simulation results show that the frequency of A_1 in the natural population is gradually increased with generation due to the increase in migrant allele frequency from artificial populations (*Figure 1a*). The frequency of genotype A_1A_1 is gradually increased with generation, while the frequencies of other two genotypes are gradually reduced. Additive and dominance variances are reduced with generation (*Figure 1b*), and so does the mean fitness (*Figure 1c*).

Case II: GIM and heterozygote disadvantage

In reality, a natural population with heterozygote disadvantage only is not stable if there are no any other forces to counteract the selection, except at a specific sate where allele frequency is 0.5 (LI, 1976). Allele A_1 can be fixed or extinct, depending upon whether its initial frequency is greater or smaller than 0.5. However, with the impacts of migration the equilibrium level of allele frequency relies on the migrant allele frequency. Such populations can be observed in hybrid zones where hybrids have lower fitness than either parent and a cline in allele frequency can be maintained (e.g. ENDLER, 1977; BARTON and HEWITT, 1985).

Consider the specific case with initial allele frequency at 0.5, which can be used as a reference for comparison with the following case under impacts of gene flow. Let W_{11}=1.0, W_{12}=0.95, W_{22}=1.0, a=d=1.0, and m_S=m_P=0. Compared with the magnitudes at HWE, heterozygote frequency is reduced, while

Fig.1a

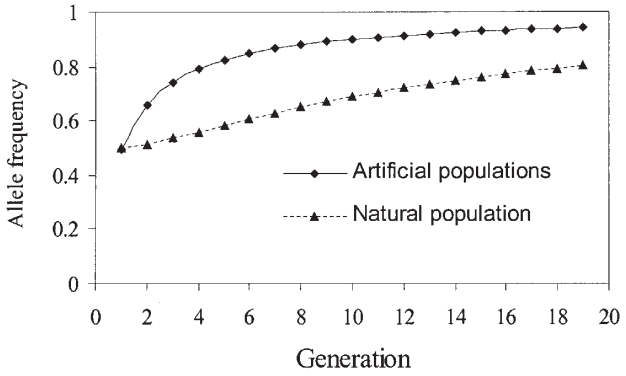

Fig.1b

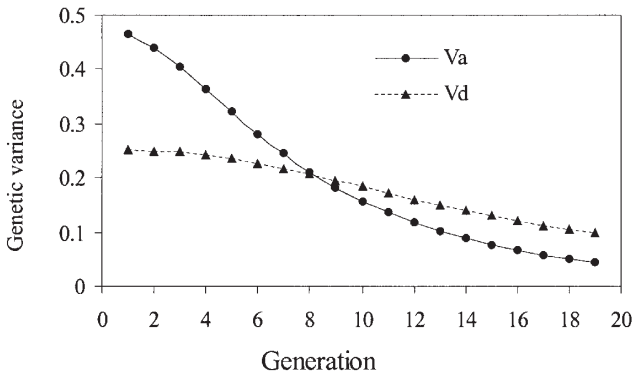

Fig.1c

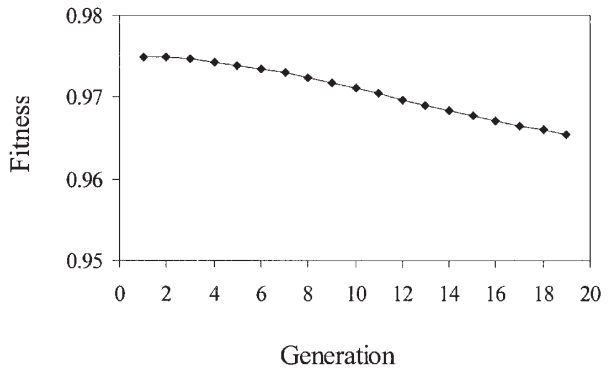

Figure 1. – Changes in different genetic parameters with generation in the case of heterozygote advantage: (a) allele frequency; (b) additive and dominance variances in the natural population; and (c) mean fitness. Parameters are W_{11} = 0.95, W_{12} = 1.0, W_{22} = 0.95, a = d = 1.0, m_s = 0.05, and m_p = 0.10. Note that changes in the frequency of A_1 in artificial populations with generation, $Q_1(t)$, are assumed.

Fig.2a

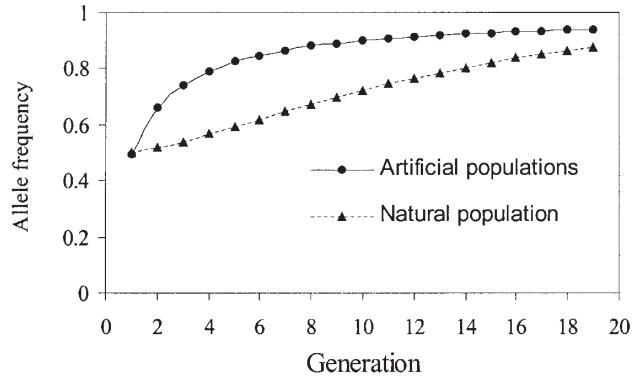

Fig.2b

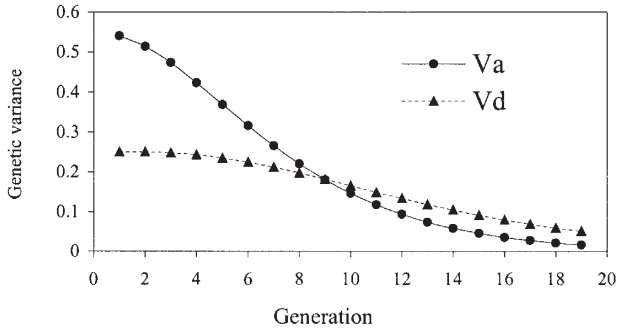

Fig.2c

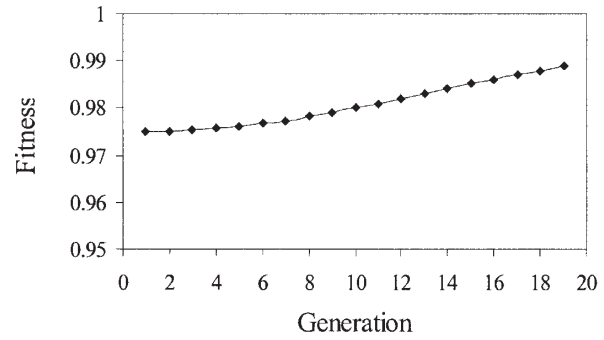

Figure 2. – Changes in different genetic parameters with generation in the case of heterozygote disadvantage: (a) allele frequency; (b) additive and dominance variances in the natural population; and (c) mean fitness. Parameters are W_{11} = 1.0, W_{12} = 0.95, W_{22} = 1.0, $a = d$ = 1.0, m_s = 0.05, and m_p = 0.10. Note that changes in the frequency of A_1 in artificial populations with generation, $Q_1(t)$, are assumed.

homozygote frequencies are increased: f_{11}=0.2564, f_{12}=0.4872, and f_{22}=0.2564. Additive and dominance variances are maintained at V_A=0.5394 and V_D=0.2505, respectively, and mean fitness is $\bar{W} = 0.975$.

When immigration from artificial populations takes place, say m_S=0,05 and m_P=0,10, the equilibrium frequency of A_1 relies on its frequency in migrants. The frequency of allele A_1 in the natural population is gradually increased with generation due to the increase in migrant allele frequency from artificial populations (*Figure 2a*). Like *Case* I, the frequency of genotype A_1A_1 is gradually increased with generation, while the frequencies of other two genotypes are gradually reduced. Additive and dominance variances are gradually reduced with generation (*Figure 2b*). Unlike Case I, mean fitness is increased with generation (*Figure 2c*).

Table 1. – The stability properties for three types of frequency-dependent selection under the case of $p_1(0) \neq 0.5$. Symbol (+ - +) stands for the three selection coefficients (s_1 s_2 s_3) with positive s_1, negative s_2, and positive s_3. Similar meanings are represented for other combinations.

Selection types	(+ - +)	(- + -)	(+ + +)	(- - -)
FDS1	unstable	stable	stable	unstable
FDS2	unstable	stable	unstable	stable
FDS3	stable	stable	stable	unstable

Case III: *GIM and frequency-dependent selection*

When initial allele frequency is not equal to 0.5 and no other evolutionary forces counteract selection, there is differential in population stability under different signs of selection coefficients (*Table 1*). Generally, there is always an equilibrium level of allele frequency (no fixation and no extinction) in the case of heterozygote advantage (*Table 1*). For example, when no immigration takes place (m_S=m_P=0), consider the specific case with initial allele frequency at 0.5, and let s_1=s_2=s_3=0.05. The equilibrium frequencies of genotypes are: f_{11}=0.2508, f_{12}=0.4984, and f_{22}=0.2508 in FDS1; f_{11}=0.2485, f_{12}=0.5030, and f_{22}=0.2485 in FDS2; f_{11}=0.2609, f_{12}=0.4783, and f_{22}=0.2609 in FDS3. Additive and dominance variances vary with selection type: with the highest additive variance in FDS3 (V_A=0.5681), and then in FDS1 (V_A=0.5046), and the smallest additive variances in FDS2 (V_A=0.4908). Dominance variance is similar in both FDS1 and FDS2 (V_D=0.2500), but smaller than the case of FDS3 (V_D=0.2514). Mean fitness is $\bar{W}$=1.0156 in FDS1, $\bar{W}$=1.0187 in FDS2, and $\bar{W}$=1.15 in FDS3.

When immigration takes place, say m_S=0.05 and m_P=0.10, genetic variances are changed with generation. Also, let s_1=s_2=s_3=0.05, and a=d=1.0. The frequency of allele A_1 is gradually increased with generation although there are differences in magnitude among different types of selection (*Figure 3a*). The frequency of allele A_1 is slightly increased with generation in FDS3, compared with those in FDS1 and FDS2. There are differences in population fitness among the three selection regimes: slight reduction with generation in FDS1, slight increase in FDS2, and almost no change in FDS3 (*Figure 3b*). The frequency of genotype A_1A_1 is increased with generation, and the frequencies of other two genotypes are reduced in both FDS1 and FDS2. This is not the case in FDS3 where genotype frequencies are maintained at approximately equilibrium levels: f_{11}≈0.48, f_{12}≈0.40, and f_{22}≈0.12. Additive and dominance variances in all three types of selection are generally reduced with generation, although there are differential in magnitude among them (*Figure 3c, d*). Higher genetic variances can be maintained in FDS3 than in other two types of selection (FDS2~3).

Discussion

The results presented here show that when artificial populations are genetically improved, erosion of quantitative genetic variation in natural populations can be substantial due to the

Fig.3a

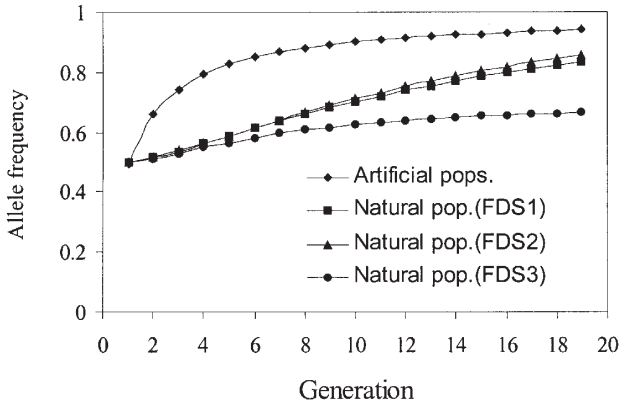

Fig.3c

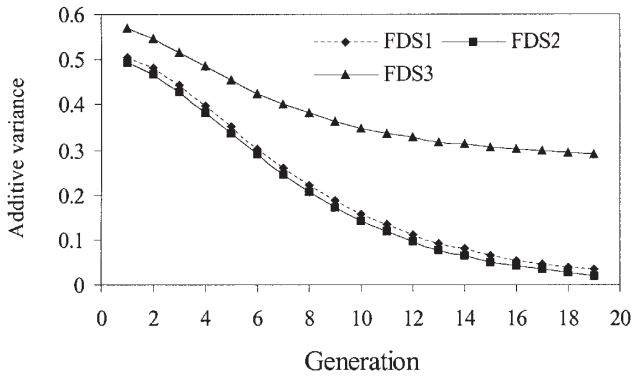

Fig.3b

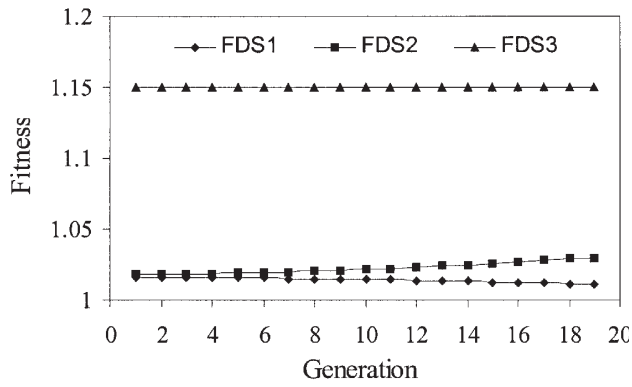

Fig.3d

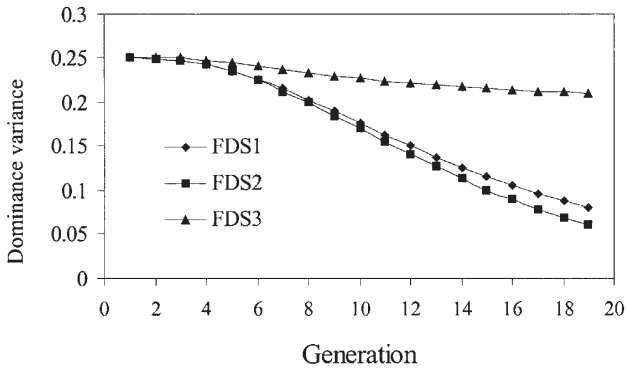

Figure 3. – Changes in different genetic parameters with generation under three types of frequency-dependent selection (FDS1~3): (a) allele frequency; (b) mean fitness; (c) additive variances; and (d) dominance variances. Parameters are $s_1 = s_2 = s_3 = 0.05$, $a = d = 1.0$, $m_s = 0.05$, and $m_p = 0.10$. Note that changes in the frequency of A_1 in artificial populations with generation, $Q_1(t)$, are assumed.

gene flow from artificial populations. However, when artificial plantations are not genetically improved, erosion of genetic variation in natural populations is small. These results generally hold, although there are differences in magnitude in eroding genetic variation under different types of selection.

Our results imply that the genetic materials used for artificial forest populations are critical in preventing erosion of genetic variation in natural forests, since gene flow is difficult to avoid in many forest tree species. In order to conserve genetic variation in natural populations, appropriate isolation of natural populations from artificial plantations is imperative. According to the function, artificial populations can be classified into several types, such as city ornamental forest, water and soil preservation plantation, and short-rotation industrial forests. The time required to maintain these artificial populations is variable, resulting in different impacts on natural populations via gene flow. Practically, the short rotation plantation for specific industrial purposes is usually replaced with the genetically improved materials when replanted. The ultimate case is to establish clonal populations where genetic gain is substantially increased, and the potential influence on natural forests is considerable.

The time required for maintenance of other types of artificial populations can be long. In this case, impacts on surrounding natural forests could also be considerable when genetically improved materials are planted on large scale. However, impacts of gene flow will not be serious when the materials for artificial populations are directly sampled from natural populations, where no significant change in gene frequency takes place. Such point is also indicated in a previous study on the genetic variation in a fish population affected by one-way gene flow (YOKOTA and WATANABLE, 1997). In addition, artificial populations with genetically unimproved materials can be seen as a type of *in situ* or *ex situ* conservation of natural populations.

Our results show there are differences between mean fitness and variance components in response to one-way gene flow. When genetically unimproved materials are used for artificial populations, both mean fitness and variance components remain unaltered, because gene flow does not significantly alter the gene frequency in natural populations. This is not the case when genetically improved materials are used for artificial populations, where gene flow via seed and pollen dispersal can bring about heterozygote deficiency in natural populations. Mean fitness is increased with gene flow in the case of heterozygote disadvantage, such as in hybrid zones (e.g. BARTON and HEWITT, 1985), but reduced in the case of heterozygote advantages. Nevertheless, both additive and dominance variances in either case are reduced due to gene flow from genetically improved populations.

According to FISHER's fundamental theorem (FISHER, 1930), natural selection increases population mean fitness per generation by a mount equal to additive variance in fitness; while

gene flow reduces it. BURT (1995) argued that pollen flow can decrease fitness by ~0.12 per generation in *Anthoxanthum odoratum*. Seed flow can reduce fitness by ~0.0045 per generation in *Impatiens capensis*. In the same species *Ipomopsis aggregata*, seed and pollen flow can reduce fitness by ~0.002 and ~0.0008 per generation, respectively. The reduction in additive variance in fitness can be indirectly predicted (BURT, 1995; BARTON, 2001). Reduction in genetic variances owing to seed and pollen flow from genetically improved populations is demonstrated in the present numerical examples.

Practically, transfer of materials from one region to another often takes place, and allele frequencies in transferred materials are often distinct from recipient populations. Although the pattern of the change in allele frequency in transferred materials at each time is difficult to determine, it may belong to the type between our two simulated cases or the mixture of our two simulated cases. Such a transfer of materials can change mean fitness and erode genetic variances in the recipient populations. One case is concerned with newly transferred materials that are more poorly adapted than local populations. This will lead to (1) an increase in the proportion of poorly adapted materials in a specific region and (2) to contaminating of locally adapted populations, resulting in seeds containing alien alleles from the new materials via pollen flow (ENNOS et al., 1998), and in reduction in adaptation.

One typical type of artificial population is that planted with materials from a seed orchard, where heterozygosity can be different from that in natural forest populations (e.g. STOEHR and EL-KASSABY, 1997). Under this situation, effects of the gene flow from large area of plantation could be substantial in eroding genetic variation in natural forests. This consequence can be explicitly implied from our numerical simulations.

Our results indicate there are differences in maintaining genetic variances among the three examined types of frequency-dependent selection, although the same trend is observed for each type in response to gene flow. The first type (FDS1) represents the relationship among different genotypes, and few examples can be found in forest tree species. The ecological mechanism for maintaining this type of selection remains difficult to explain in forest tree species. The second type (FDS2) describes a positive relationship between one genotype fitness and its frequency: individuals of the same genotype have large fitness when having large frequency, and vice versa. Gene flow from genetically improved materials can favour homozygotes over heterozygote, resulting in the response trend similar to *Case* II. The third type (FDS3) represents a negative relationship between one genotype fitness and its frequency, and selection favours rare genotypes. In this case, impacts of gene flow from genetically improved materials are not as large as the other types of selection. Practically, the significance of the frequency-dependent selection in animal species has been stressed (e.g. HEINO et al., 1998), but remains to be explored in tree species (GREGORIUS and BARADAT, 1992). Nevertheless, the present demonstration indicates there is a similar trend in genetic variation between frequency-dependent and -independent selection in response to the gene flow from genetically improved materials.

Attention to several assumptions underlying the present one-locus model is required. First, a constant migration rate is assumed, which often does not occur in reality and hence can result in different extents of erosion. However, the erosion of genetic variation in recipient populations may still be brought about due to the gene flow from genetically distinct populations. Second, the assumption of no genetic drift effects could be violated when the natural population is too small. In a small natural population, impacts of gene flow could be more serious, and the adaptive alleles might even be swept out when migration rate is greater than selection coefficient (WRIGHT, 1969). Third, the assumption of random combination between pollen and ovules can also be violated since partially or predominantly selfing systems of mating are extensively observed in many plant species. Under this case, impacts of gene flow can also be strengthened in partially selfing population. With the predominantly selfing species, impacts of gene flow are realized via the dispersal of seed rather than pollen grains. Forth, our numerical examples are based on two-allele case although the model of multiple alleles is proposed. In the genetically improved populations, the alleles that have large effects on the quantitative trait of interest can be maintained at high frequency, and so does the frequencies of these specific alleles in migrants. Like the two-allele case, erosion of genetic variation remains present due to the homogenizing function of gene flow.

Finally, we must acknowledge that the genetically improved material referred to in the present model is generally characterized by the increase of the frequencies of alleles of interest. It can be generated through different breeding strategies that mainly focus on accumulating the additive effects of the alleles of interest, such as backcross breeding. However, many other breeding designs that emphasize non-additive effects of QTLs, such as hybrid and clone breeding, can generate breeding and productive populations with more complicated allelic structures (ZOBEL and TALBERT, 1984). The differential in allele frequency between natural and artificial populations could fluctuate with generation. Correspondingly, fluctuation in the reduction of genetic variances in natural populations can also be brought about.

Acknowledgements

We thank one anonymous referee for very helpful comments on early version of this article and Dr. JANE REID for editorial assistance. The work was financially supported by a grant from North Carolina State University-Industry Cooperative Tree Improvement Program.

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Short Note: Delayed Graft Incompatibility in Heteroplastic Interspecific Graft Between *Tectona grandis* L.f. and *Tectona hamiltoniana* Wall After Three Decades

By V. K. SHARMA[1]) and D. P. UNIYAL[2])

Division of Genetics and Tree Propagation, Forest Research Institute (ICFRE)
Dehradun (Uttaranchal) – 248 006 (INDIA)

(Received 27th September 2002)

Summary

Extremely delayed graft-incompatibility and mortality of interspecific heteroplastic grafts of *Tectona grandis* and *T. hamiltoniana* after three decades has been reported. Possible causes of incompatibility have been discussed.

Key words: Graft-incompatibility, Heteroplastic grafts, *Tectona grandis, Tectona hamiltoniana.*

In the year 1966–68 under the project "Genetic Improvement of Teak (*Tectona grandis* L.f)" studies for standardization of technique for vegetative propagation of plus trees were undertaken and wedge and cleft grafting and bud grafting techniques were standardized (RAWAT and KEDHARNATH, 1968). Development of these techniques subsequently helped in establishment of model Clonal Seed Orchard at New Forest, the campus of Forest Research Institute, Dehradun.

During the course of these studies autoplastic, homoplastic and heteroplastic grafts were made to study the compatibility of stock-scion in different stock-scion combinations.

Five wedge and cleft grafts each of the above mentioned three types were made on field grown stock of *Tectona grandis* Lf, in the year 1966–68. Interspecific heteroplastic grafts were made using the scion material collected from mature trees of *Tectona hamiltoniana* Wall, growing in the campus of this Institute. These heteroplastic grafts which were successfully established did not show any sign of graft incompatibility at their early growth period of 10 years but gradually they started developing symptoms of graft incompatibility such as saddle like outgrowth of scion at the junction of stock and scion (*Fig. 1*). These interspecific heteroplastic grafts died one by one between the age of 25 to 32 years when the symptoms of graft incompatibility became more pronounced. The oldest graft could survive upto 32 years. At this age the graft attained a height of 5 m, girth of scion 76 cm (at the junction of graft union) and girth of stock 64 cm. It would be worth to mention here that none of the grafts flowered till they survived.

Heteroplastic or interspecific grafting is used in fruit tree breeding to produce small trees with early and rich flowering. The same effect is aimed at when grafting forest trees for seed orchards establishment (DORMLING, 1964). Problems of graft incompatibility or uncongeniality of stock and scion have been reported in a number of horticultural and forest tree species (MOSSE, 1962, HARTMANN and KESTER, 1968, COPES, 1970, WRIGHT, 1972, TUBBS, 1973, HARTNEY, 1980, ZOBEL and TALBERT, 1984) and have been the subject of many investigations (PROEBSTRING, 1926, 1928, BRADFORD and SILTON, 1929; MC CLINTOK, 1948, HERRERO, 1951, THREL, 1954, STIGTER, 1956, and PITCHER, 1960).

It is a common occurrence that the scion may persist for few months, one or more years and then die. SCHONBACH (1960) reported that some grafts of *Populus* lived upto 7 years. Anatomical investigations carried out on these grafts have revealed that in these grafts xylem unions were almost complete but phloem junctions were unsatisfactory. EMMANUEL and BAGCHI (1984) observed the phenomenon of graft incompatibility with certain clones of *Tectona grandis* in homoplastic grafts. Studies carried out in Sweden on heteroplastic grafting in

[1] Research Officer

[2] Head, Division of Genetics and Tree Propagation