Linking Evolutionary Quantitative Genetics to the Conservation of Genetic Resources in Natural Forest Populations

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Abstract

Current decision-making on conservation of genetic resources has not been well fused with evolutionary quantitative genetics, which can provide new insights into the "dynamic conservation" of gene pools. With the assumption of no epistasis at QTLs (quantitative trait loci), alleles of unequal effects can be maintained at different levels of polymorphism in natural populations. However, at adaptive QTLs, rare alleles of large effect cannot contribute much adaptation to future environment changes. Rather, QTLs of small effect play a major role in creating genetic variation of adaptive quantitative traits, and mediating future adaptive changes. Owing to the impacts of mating system and to differences of mutation rates between markers and QTLs, the information provided by molecular markers is not that helpful for guiding conservation of quantitative genetic variation. Also, the genetic properties of QTLs allowing *in situ* conservation of quantitative genetic variation need to be better understood. Although some methods for *ex situ* conservation of "continuous evolutionary potential" are not static, they are not the same methods as used for *in situ* conservation. The conceptual method of "dynamic conservation" should be given a priority because of the temporally and spatially fluctuating environments where forest trees grow.

Key words: Genetic conservation, evolutionary quantitative genetics, genetic resources, natural forest populations, quantitative trait loci.

Introduction

Knowledge of population genetic structure can be crucial for decisions about the sustainable management of forest genetic resources. Since different pictures of population genetic structure are often provided by molecular markers versus adaptive quantitative traits, integration of both kinds of information should be used to develop strategies for the genetic conservation of tree species (HU *et al.,* 2000). Moreover, effective geographical isolation of natural populations from artificial populations is also important, since gene flow homogenizes the genetic divergence between populations. A potential reduction of genetic variation in natural populations can be brought about when gene flow occurs from artificial populations that are genetically improved and characterized by a substantial increase of the alleles of interest (ELLSTRAND *et al.,* 1999; HU *et al.,* 2001). In this article we examine how evolutionary quantitative genetic theory can be used to develop strategies relevant to management of genetic resources.

Quantitative genetics can provide an important contribution to genetic conservation strategies for the following reasons. First, many quantitative traits are of economical significance, and some are strongly associated with population adaptation to different environments. At QTLs (quantitative trait loci), alleles often affect traits of adaptive or economic significance, and quantitative genetic variation is often concentrated in tree improvement and conservation programs. Second, compared with artificial plantations, natural populations have many specific features, such as high heterozygosity and large genetic load, for which evolutionary quantitative genetics can be applied, and used to evaluate and develop strategies for conservation of quantitative genetic variation in natural status. While the science of biodiversity has been often applied to the management of biodiversity, the science of evolutionary quantitative genetics has not been extensively applied to the conservation of genetic resources in natural populations.

Although there are extensive studies on quantitative genetic theory (FALCONER and MACKAY, 1996; LYNCH and WALSH, 1998), more studies on the maintenance of quantitative genetic variation in natural populations are required. Nevertheless, some hypotheses for explaining the evolutionary processes of quantitative traits, such as the stabilizing selection hypothesis and the balance of mutation/selection, are commonly accepted. BARTON and TURELLI (1989) and WHITLOCK *et al.* (1995) gave detailed reviews on quantitative genetics. In this article, we will briefly review additional theories relevant to conservation of quantitative genetic variation in natural populations. Our aims are to bridge the gap between evolutionary quantitative genetics and conservation of natural populations, to improve our understanding of the dynamics of quantitative genetic variation in natural status, and to assess the conservation *in situ* and *ex situ* that are currently employed in practical conservation programs.

Factors influencing the evolution of quantitative traits

Quantitative traits display a continuous, often normal (Gaussian) distribution, for which the classical multiple-factor hypothesis (many factors each with equally infinitesimal effect) is used to describe the genetic bases for such phenotypic variation. This hypothesis is now challenged by many findings that QTLs with unequally large effects underlie many quantitative traits, in both plants and animals (e.g. GRATTAPAGLIA *et al.,* 1995; MACKAY, 1995). Nevertheless, like those of individual Mendelian characters, evolution of quantitative traits is also affected by many similar factors.

WRIGHT (1949, 1955) classified these factors into three general kinds: (i) systematic change, (ii) random change, and (iii) environmental change (*Table 1*). These factors are directly or indirectly associated with changes in gene frequency and hence in quantitative genetic variation in natural populations. However, the relative impacts of each factor may vary by QTL and quantitative trait. For example, mutation contributes little to the genetic variation of a quantitative trait in short-term evolution, but this effect cannot be ignored in long-term evolution. Compared with agricultural crops, herbivores, and parasites, forest trees grow in temporally and spatially fluctuating environments and have several specific features, such as long generation cycle, high genetic load and environmental heterogeneity (HATTEMER, 1995). Simultaneous impacts of these

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Table 1. – Factors influencing quantitative genetic variation and the related human activities and natural events.

Factors	Human activities	Natural events
Systematic change		
a. Recurrent mutation		Steady radiation.
b. Migration and crossing	Pollen and seed introduction; hybridization.	Wind- or animal-dispersed pollen and seed.
c. Mass selection	Logging.	Natural thinning.
Random change		
a. Random mutation	Unreasonable disposal of radiation materials.	Unsteady radiation
b. Random migration	Irregular pollen and seed transfer	Stochastic dispersal of seed and pollen
c. Random selection	Grazing, non-timber harvest	Natural selection, food chain
d. Genetic drift	Non-timber logging	Fire, disease, and pests disaster
Environmental change		
a. Natural succession	Slash-and-burn system, exotic forestry	Natural adaptation change; changes in ecological niches
b. Environmental gradient	Industrialization, fragmentation	Air pollution, climate change

factors on quantitative genetic variation in trees can take place via human activities or natural events (*Table 1*).

An overview of some evolutionary genetic theories

Basic evolution equation

An evolution equation describes the change per generation in the mean of a quantitative trait. FISHER's (1930) fundamental theorem of natural selection provides a general prototype for related other studies (e.g. KIMURA, 1958). HALDANE's (1957) cost of natural selection theory, WRIGHT's (1977) shifting balance theory (SBT) (COYNE *et al.,* 2000; GOODNIGHT and WADE, 2000), and other evolutionary theories improve our understanding of population evolution.

Generally, two approaches have been used in modeling phenotype evolution of quantitative traits in natural populations. One is to model evolution by avoiding a reference to gene frequency (phenotype approach). The other is to model phenotype change with a complete genetic analysis in terms of gene frequency and genotype composition (NARAIN, 1993; LANDE, 1988). Some results for the change in means of multiple traits under the assumption of additive effects are outlined in *Table 2*. Equations for the moments higher than the second order and for the case with epistasis can be found in BARTON and TURELLI (1987), TURELLI (1988), and TURELLI and BARTON (1990). A common feature in these equations is that genetic variances and covariances are crucial components for quantitative trait evolving ability.

QTL fixation and extinction

One of the objectives in genetic conservation is to ensure that functionally useful alleles will be available when required (NAMKOONG, 1997). Availability of a targeted allele is related to its fate in nature populations. Behavior of individual loci under the assumption of no epistasis among loci has been studied (WRIGHT, 1969; KIMURA, 1964), and some results are also suitable for QTLs in nature populations under certain conditions. If the selection coefficient (s) of a new QTL mutant is small (weak) in a population with N number of individuals, fixation probability of the mutant, $u(1/(2N))$, can increase when population size is reduced (*Figure 1*). Mean extinction time of the mutant, $\bar{t}_0(1/(2N))$, can substantially increase with population size (*Figure 2*).

In natural populations, the relationship between selection coefficient (s_i) of an allele and its additive effects (a_i) on phenotype can be approximated by $s_i = a_i I/\sigma_P$ where I is the selection intensity and σ_P is the phenotypic standard deviation (KIMURA and CROW, 1978; HILL, 1982). This relationship is valid in the case of either directional or stabilizing selection (KIMURA and CROW, 1978). Concerning the selectively neutral QTLs with unequally large effects (LANDE, 1976), there will be no significant divergence among them in fixation probability and extinction time. However, adaptive QTLs with large effects have large selection coefficients, and the fixation probability may be large (*Figures 1* and *2*). New mutants of QTLs with large effects are often deleterious and even lethal due to malfunction, and will be eliminated by natural selection. As a consequence, QTLs with large effects often have low polymorphism in natural populations, say allele frequency greater than 0.95 or less than 0.05. In contrast, many QTLs with small effects have small selection coefficients, and their fixation probabilities are small (*Figures 1* and *2*). High polymorphism, say allele frequency around 0.5, is then likely maintained.

Table 2. – Evolution equations for polygenic quantitative traits under different models.

Models	Equations	References
I. Phenotype approach		LANDE (1988)
a. Natural selection	$\Delta\bar{\mathbf{z}} = \mathbf{A}\,\nabla \ln \overline{W}$	
b. Genetic drift	$\frac{\partial \Phi}{\partial t} = -\sum_{i=1}^{m} \frac{\partial}{\partial \bar{z}_i}(\Delta\,\bar{z}_i \Phi) + \frac{1}{2}\sum_i \sum_j \frac{\overline{A}_{ij}}{N_e} \frac{\partial^2 \Phi}{\partial \bar{z}_i \partial \bar{z}_j}$	
II. Gene frequency approach		NARAIN(1993)
a. Truncation selection	$\Delta\bar{\mathbf{z}} = \mathbf{A}\mathbf{P}^{-1}\,\Delta\mathbf{M}$	
b. Stabilizing selection	$\Delta\bar{\mathbf{z}} = -\mathbf{A}(\mathbf{w}+\mathbf{P})^{-1}\,(\mathbf{M}-\mathbf{z}_{\text{opt}})$	

$\mathbf{z}$ is a vector of m traits, $\mathbf{z} = (z_1, z_2, ..., z_m)'$; $\Delta\bar{\mathbf{z}}$ is the increment of mean vector $\mathbf{z}$; $\overline{W}$ is mean population fitness; $\nabla = (\partial/\partial z_1, \partial/\partial z_2, ..., \partial/\partial z_m)$; $\mathbf{A}$ is additive genetic variance-covariance matrix of m traits; $\mathbf{P}$ and $\mathbf{w}$ are respectively the variance-covariance for the density distribution of m traits in the population of interest and for the fitness distribution of m traits; Φ is the probability density for $\bar{\mathbf{z}}$ at time t; $\Delta\mathbf{M}$ is the directional change in mean of m traits; and $\mathbf{z}_{\text{opt}}$ is optimal values of m traits for fitness.

When QTLs have unequally large effects, the allelic distribution for a quantitative trait should be strongly associated with the metabolic pathways that lead to the trait formation (WRIGHT, 1968). The numbers of such QTLs would vary considerably with trait, depending upon how complicated the metabolic pathway is (e.g. BYRNE *et al.,* 1996). In many cases, few QTLs with large effects are present in quantitative traits, and the distribution of gene effects will probably be of an exponential kind (ROBERTSON, 1967; MACKAY, 1995, 2001). The exponential distribution roughly represents a feature of quantitative genetic variation in many traits. Therefore, it is important to understand the relative roles of QTLs with large effects versus small effects in practical conservation.

Input of QTLs genetic variance

Input of genetic variance owing to mutation creates genetic basis for population adaptation to different environments. Since many QTLs with different genetic properties are involved in the formation of a quantitative trait, their relative contributions to total genetic variation are varied. Several features for

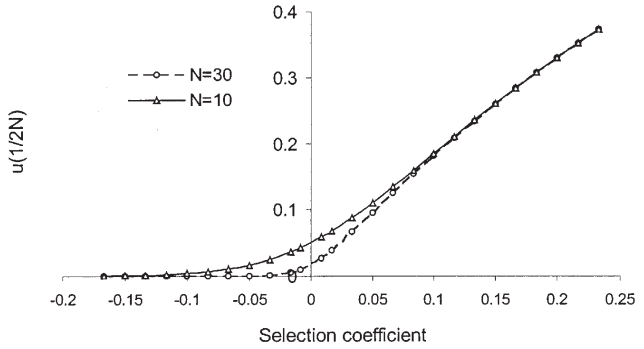

Figure 1. – Changes in the fixation probability of a mutant allele, $u(1/(2N))$, with selection coefficient (s) in a natural population with N number of individuals, under assumptions of selection, drift, mutation, but no migration. Calculation is based on KIMURA's formula $u(1/(2N)) = (1-e^{-2N_e s/N}) / (1-e^{-4N_e s})$ and the condition of $N = N_e$ (KIMURA, 1962).

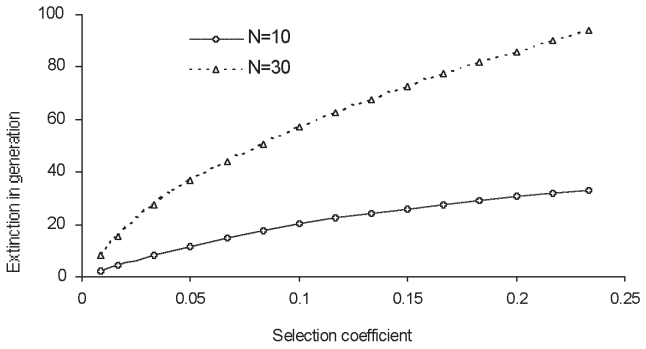

Figure 2. – Changes in the extinction time of a mutant allele, $\bar{t}_0(1/(2N))$, with selection coefficient (s) in a natural population with N number of individuals, under assumptions of selection, drift, mutation, but no migration. Calculation is based on KIMURA's formula $\bar{t}_0(1/(2N)) = (4N_e/(2N-1))\ln(2-N)$ and the condition of $N = N_e$ (KIMURA, 1969).

the role of QTL mutation in generating quantitative variation in *Drosophila* and other species can be outlined (LYNCH and WALSH, 1998). (i) Effects of mutation can be nonadditive. Mutations of QTLs with large effects are nearly recessive, while mutations of QTLs with small effects are nearly additive on average, but have variable levels of dominance (MACKAY *et al.,* 1992; CABALLERO and KEIGHTLEY, 1994; FRY *et al.,* 1995). (ii) Pleiotropic effects of QTLs with large effects can take place. (iii) Mutational effects can be symmetrical but highly leptokurtic, with a few QTLs having large effects and mean effects of being approximately equal to zero. (iv) Mutation rate of QTLs with small effects is much higher than the rate of QTLs with large effects. (v) Mutants with selection coefficients on the order of $1/(2N_e)$ are highly vulnerable to random genetic drift, but still have significant effect on fitness.

In theory, there are several models on the input of genetic variance owing to mutation (*Table 3*). These models provide a basic relationship between mutation and genetic variance, although assumptions are additive effects of mutants (no epistasis) and no distinction between QTLs with large and small effects (e.g. HILL *et al.,* 1988,1989). Practical estimation indicates that input of genetic variation by mutation is about the order of 10^{-3} times environmental variance and the total mutation rate per quantitative trait rather than per a locus is about 0.1 (LYNCH and WALSH, 1998).

Understanding the quantitative genetic variation in natural populations

There are many QTLs per trait, located across the genome, but their fates are varied, depending on the relative influences of differently evolutionary forces (*Table 1*). In this section, the genetic variation of quantitative traits in natural populations will be briefly analysed from the following aspects: the impacts of effective population size, the number of QTLs, behavior of rare allele, and genetic variance.

Impacts of effective population size

Effective population size is the size of an ideal population with the same sampling variance of allelic frequencies per generation, i.e. variance effective population size. There are also other definitions, such as the inbreeding effective population size (WRIGHT, 1969). In small populations, genetic variances for differently neutral QTLs are lost at the same rate by random genetic drift, but the replenishment of variance is varied with mutation rate (LANDE, 1999). Deleterious alleles of adaptive QTLs would be eliminated, or have small probabilities to be fixed. Alleles with large selection advantage have great probabilities to be fixed. Genetic variation is mainly attributable to those QTLs with moderate selection coefficients, say slightly greater than $1/(2N_e)$.

In large populations, genetic variances for neutral quantitative traits are caused by those QTLs with both large and small effects. For adaptive quantitative traits, deleterious (or advantageous) alleles would be eliminated (or fixed) with great probabilities even if mutation can make these alleles at very low levels of polymorphism. QTLs with large effects would not account for too much in total genetic variation in natural populations. A major proportion of genetic variation mainly comes from those QTLs with intermediate allele frequencies.

Number of QTLs

The number of QTLs contributing to the variation in a quantitative trait provides another aspect of useful information in

Table 3. – The relationships between quantitative genetic variances and mutation under different models.

Models	Genetic variances	References
I. Neutral case	$V_G = 2N_eV_M$, $V_M = nuE(a^2)/2$	CLAYTON and ROBERTSON (1955)
(multiple additive QTLs)		
II. Stabilizing selection		
Continuum-of-alleles	$V_G = n[uE(a^2)V_S]^{1/2}$	KIMURA (1965)
Multi-allelic model	$V_G = 4nuV_S$	TURELLI (1984)
(House-of-Cards)		
Continuum-of-alleles	$V_G = \frac{4nuV_S}{1+V_S/N_ea^2}$	BÜRGER *et al.* (1989)
and House-of-Cards		KEIGHTLEY *et al.* (1988)

V_G: genetic variance; V_M: mutation variance; n: number of QTLs; u: mutation rate; a: additive effect per locus; V_S: an inverse measure of the strength of the stabilizing selection for genotypic value; $E(a^2)$: mean value of a^2.

understanding genetic architecture of quantitative variation. Based on artificial populations (P_1, P_2, F_1, F_2, BC_1, and BC_2), the number of independently segregating pairs of QTLs alleles can be approximately estimated under a variety of assumptions on the gene effect distribution (WRIGHT, 1968; LANDE, 1981). Currently, the maker-based method is widely used to detect QTLs with large effects (LYNCH and WALSH, 1998), but the method based on natural populations remains to be developed.

One important question is concerned with the stability for the number of QTLs with large effects in a quantitative trait. The number of independent QTLs with small effects should be infinite (WRIGHT, 1968); whereas the number of QTLs with large effects should be limited and would be likely dynamic under fluctuating environments and/or different development stages (LYNCH and WALSH, 1998). More QTLs with unequally large effects would complicate the conservation program that simultaneously conserves genetic variation of multiple major QTLs.

Is a rare QTL allele important?

The results for the number of alleles that can be maintained in a finite population (KIMURA and CROW, 1964) are also suitable for QTLs with some genetic properties. Origination of a rare allele results from actions of differently evolutionary forces. Genetic drift is responsible for the formation of rare alleles of neutral QTLs; whereas the balance of selection/mutation is mainly responsible for the formation of a rare deleterious allele even though there is a small probability for the deleterious allele to be fixed due to large genetic drift. The probabilities for adaptive alleles to become rare alleles are very small (*Figures 1* and *2*). Thus, rare alleles of functional QTLs in many cases are due to poor local adaptation and not useful for population adaptation to environment change in the future. Therefore, rare alleles of adaptive QTLs are often not important and can be ignored in genetic conservation.

However, maintenance of a rare allele with large effect is required when it is of significant value or of disease resistance. Furthermore, rare alleles poorly adaptive to one local environment would likely become adaptive to another local environment or become so in the future when global climate changes. From this point of view, conservation of rare QTL alleles requires emphasis.

QTLs in population evolving ability

Maintenance of genetic variance can strengthen the potential for population evolution (*Table 2*). As mentioned in the preceding section, genetic variance is mainly originated from the accumulation of mutation by creating new alleles and changing gene frequency. Genetic variances are function of allele frequencies and QTLs effects (FALCONER and MACKAY, 1996). The effect of a given allele is relatively stable in long-term conservation, but allele frequencies are not. QTLs with large effects would not be shifted into QTLs with small effects under a constant environment. Therefore, the maintenance of quantitative genetic variance is actually shifted into the maintenance of allele frequencies with high polymorphism.

Adaptation to future environment changes mainly results from those alleles that are currently of high polymorphism (HOLSINGER *et al.,* 1999). As long as a large genetic variance can be maintained, quantitative traits will evolve at an adequate rate (*Table 2*). Based on the genetic properties of QTLs mentioned in the preceding section, it can be inferred that genetic variances for adaptive quantitative traits are mainly due to QTLs with small effects rather than those with large effects.

Molecular markers and QTLs

Currently, detection of QTLs with large effects is mainly achieved by associating molecular markers with quantitative traits. However, there are several constraints that limit the application of molecular markers in natural populations for the purpose of conservation. Marker-based methods are only effective for those populations that create tight linkage between markers and QTLs. Such prerequisite condition can be met in many artificial populations, but is rarely met in natural populations. Most tree species, e.g. many conifers (MITTON, 1992), are predominantly outcrossing, and linkage disequilibria between loci are often weak. Molecular markers linked to QTLs in artificial populations would not be linked to the same QTLs in natural populations. Therefore, markers would be likely useful only in predominantly selfing tree species where linkage disequilibrium can occur in natural populations.

Genetic properties between molecular markers and QTLs are not the same. (i) Mutation rate is much higher for QTLs with small effects (10^{-4} to 10^{-3} per generation) than for molecular markers (10^{-8} to 10^{-5} per generation for nucleotide sequence and restriction-site). Thus, the evolutionary dynamics for molecular markers cannot be well used to predict the evolution of adaptive quantitative traits (HOLSINGER *et al.,* 1999). (ii) Mechanism for maintaining genetic variation is different: mutation/drift for selectively neutral markers, and mutation/selection/drift for adaptive QTLs. The relationship between neutral markers and adaptive QTLs, such as hitchhiking effects, remains difficult to elucidate. (iii) In many cases, QTLs with large effects can be statistically detected with molecular markers. As mentioned before, QTLs with large effects would not contribute too much to future adaptation because of their low polymorphism. The linkage between molecular markers and QTLs with relatively small effects should be crucial, but is difficult to detect due to low statistical power. Therefore, a great care must be taken when molecular markers are applied to conservation of quantitative genetic variation.

Maintaining the evolutionary potential in conservation

The goal of genetic conservation is to maintain genetic variation and to conserve the evolutionary potential. Natural populations are always in dynamic status due to the impact of many factors (*Table 1*). An important requirement in conserving quantitative variation is to maintain its dynamics (NAMKOONG, 1998). Maintenance of continuing evolution should be primarily emphasized in developing conservation strategy.

Conservation *in situ* is conducted "on site", within original ecosystem where the populations under study occur, or on the site formerly occupied by that system. It also includes artificial regeneration whenever planting or sowing is done without conscious selection and in the same area where materials are collected (FAO, 1993a). In contrast, conservation *ex situ* is conducted outside natural distribution of parent populations (off site) in gene banks as seed, tissue or pollen, in plantation, or in other live collection (FAO, 1993a). The advantages and disadvantages between conservation *in situ* and *ex situ* have been compared in detail (FAO, 1993a, b; PURI, 1998). The theoretical analyses mentioned in the third and the forth sections of this article can be applied to conservation *in situ*. The evolutionary potential can be maintained when the population *in situ* is sufficiently large.

The effectiveness of conservation *ex situ* in different forms has been evaluated (e.g. FAO, 1993b; HATTEMER, 1995; PURI, 1998). Conservation *ex situ* in the forms of seed bank, pollen bank, and tissue bank, called static conservation, decouples from dynamic environments and implies a risk of accumulation

of genetic load (HATTEMER, 1995). For example, seed quality of threatened dryland palms *Hyphaene thebaica, H. petersiana* and *Medemia argun* under conventional seed bank conditions is not yet guaranteed, and changes in several seed physiological traits were observed (DAVIES and PRITCHARD, 1998). By simulating aging experiment, EL-KASSABY and EDWARDS (1998) also suggested that genetic contribution of seedlots might be changed with seed age during long-term storage, and the reliance on seed banks for conservation *ex situ* requires evaluation.

When sufficient sample size can be obtained, genetic variation in seed bank can be maintained at the approximately same level as in source populations. After long-term conservation *ex situ*, genetic variation for QTLs would be potentially divergent from the source populations that are maintained *in situ*. Compared with the source populations maintained *in situ*, "adaptive lag" to environment could occur when the materials maintained *ex situ* were reused. Input of QTL genetic variation due to mutation should be very small during long-term static conservation. Adaptation of materials in static conservation would be affected by the condition in storage and the time lasted. Poorly adaptive alleles are not eliminated during the period of storage, and will likely present maladaptation in the future. Thus, a large genetic differentiation between populations maintained *ex situ* and *in situ* is expected, especially for QTLs with large or adequate effects.

A conservation stand *ex situ* is a type of dynamic conservation (HATTEMER, 1995). However, its genetic divergence from natural populations depends on how the stand *ex situ* is established, including impacts of sample size, phenotype selection criteria, and choice of planting site. Provided that sample size is sufficiently large, genetic drift effect can be ignored. If all individuals are chosen randomly from natural populations, there will be no initially significant genetic differentiation between the stand *ex situ* and natural populations. The genetic differentiation is mainly created due to natural selection after planting. The stand *ex situ* often suffers from hard natural selection, and deleterious alleles with large effects would be eliminated quickly. Mean quantitative trait in question in the stand *ex situ* would differ from that in natural populations. If there is significantly heterogeneity in environmental factors between the stand *ex situ* and natural populations, genetic differentiation for adaptive QTLs will be even increased.

If all individuals in a stand *ex situ* are chosen according to the phenotype performance in natural populations, rare alleles of QTLs with large effects will be eliminated with a great probability. Such consequences are similar to the impacts of artificial logging on natural populations (RATNAM *et al.,* 1999). Advantageous allele frequencies of QTLs with large effects would be much higher in the stand *ex situ* than in natural populations. However, genetic variance within the stand *ex situ* is reduced, and large deviation from natural populations in genetic variation is initially created. Therefore, distinction between conservation populations *ex situ* and *in situ* is clearly important in developing strategy for maintaining the evolutionary potential of genetic resources.

Conclusions

Evolutionary quantitative genetics can improve our understanding on the genetic variation of quantitative traits in natural populations, and help to assess some conservation strategies. Several conclusions can be outlined as follows.

(i). The magnitude of genetic variance in natural populations is an important component in driving evolution of quantitative traits and in conservation;

(ii). In many cases, extinction of deleterious alleles of QTLs with either small or large effects occurs, and most adaptive QTLs alleles of large effect are fixed with high probability;

(iii). More QTLs of large effect complicates a conservation program that simultaneously conserves genetic variation for multiple QTLs. Whether or not the number of QTLs with large effects is a stable remains to be studied, but the number of QTLs with minor effects should be infinite;

(iv). Input of genetic variance owing to mutation is mainly attributable to those QTLs with small effects. Adaptive QTLs with large effects usually do not contribute too much to the total genetic variation because of low polymorphism, and need not much care in conservation;

(v). Rare QTL alleles in current populations are generally not important for population adaptation to future environment changes;

(vi). There are several constraints for the use of molecular markers to guide conservation of genetic resources;

(vii). Maintenance of continuing evolution should be given a priority in developing a conservation strategy. The distinction between *ex situ* and *in situ* conservation is important in developing strategy for maintaining the evolutionary potential of genetic resources.

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Variation Between Single Tree Progenies of *Fagus sylvatica* in Seed Traits, and its Implications for Effective Population Numbers

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Abstract

Variation between families in seed production, germination, dormancy and weights were studied in beechnuts collected from 20 individual beech (*Fagus sylvatica* L.) trees from a Danish stand, two different years (1993 & 1995). Combined cold treatment and germination at 5 °C was compared with cold treatment for 5, 7 and 9 weeks and germination at 15 °C. Finally, the effect of the pericarp on variation and level of dormancy was studied.

Significant family differences in seed weight, germination percentages, mean germination time (dormancy) and seed production were found. No simple correlation between germination and dormancy was observed: the correlation between germination and germination time was zero in 1993-seed lots, whereas there was observed a significant correlation between

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