POPULATION GENETICS THEORY IN MANAGING NATURALLY REGENERATED FORESTS

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Abstract . - -Three subjects related to application of population genetics theories in managing naturally regenerated populations (NRP) are discussed in this paper. The first subject deals with principles involved in such application. The main function of population genetics in management of NRP, availability of useful population genetics information, and information needed are discussed. The second subject deals with examining the significance of selective thinning or harvesting in a NRP. It is concluded that even if we fail to detect the significant difference between selected and unselected populations, the artificial selection on a quantitative trait could seriously change the genetic properties of the NRP. The third subject deals with detection of allele frequency changes from the selection on a quantitative character. It is demonstrated that even if a quantitative trait shows a statistically significant difference between two populations, it is unlikely that significant allele frequency change will be observed.

Additional keywords : Artificial selection, Industrial melanism, allele frequency change, black cherry, Scots pine.

Population genetics theories have been frequently applied in forest genetics research. Due to the past emphasis on artificial regeneration, quantitative genetics received most attention in forest genetics research. In this case population genetics theories were applied indirectly via quantitative genetics. Recently, population genetics theories have been used directly to determine size and structure of breeding base populations for long-term tree breeding (Namkoong et al. 1980, Kang and Nienstaedt 1987). Since the emergence of electrophoretic technique, forest geneticists have used population genetics theory to study evolution and/or classification of natural forest tree populations.

While geneticists have worked on artificially regenerated populations (ARP) or natural populations (NP), silviculturists and forest managers have influenced genetic properties of naturally regenerated populations (NRP). In NRP the genetic structures are artificially changed through selective or clear cutting, but in NP no human action is involved. A few publications dealing with genetic changes in NRPs exist, but papers that apply population genetics theories to management of NRPs have not been found. Furthermore, little is known about the usefulness of population genetics theories in managing NRPs.

In this paper I will discuss three subjects: (1) The value of applying population genetics theories in managing NRPs, (2) significance of artificial selection, such as selective thinning or harvesting, in a NRP, and (3) detection of allele frequency changes from selection on quantitative characters.

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APPLYING POPULATION GENETICS THEORIES IN MANAGING NATURALLY REGENERATED POPULATIONS

Before addressing the value of population genetics, I will briefly discuss the need for forest genetics input in managing NRPs. Two concerns have prompted the interest in genetics input in NRPs: (1) The changing genetic quality of NRPs could have a significant impact on the national productivity of timber. On a per acre basis, the potential genetic change might be trivial, but the amount of land regenerated through natural regeneration far exceeds that through artificial regeneration, especially in the Northeastern USA (Murphy and Kang 1985). (2) The National Forest Management Act of 1976 (USDA 1979) mandated the USDA Forest Service to practice multiple resource management. Subsequent National Planning Regulations (USDA 1982) introduced "diversity" as a criterion to be considered. These regulations influence how the National Forest Systems manage their timber resources. Because timber represents genetic resources, geneticists must assist managers by explaining genetic consequences of different management actions. Consequently, these regulations can be interpreted as requiring conservation of genetic resources as a criterion for forest management.

These concerns are quite different from that for ARP, where maximizing short-term economic gain per unit area has been the primary guiding principle. Because the population(s) of interest is small in ARP, breeders can intensively study and manage the reference population, where the management includes controlling environments as well as genetic stocks.

From the comparison of the justifications for forest genetics research, we can readily conclude that the type and intensity of genetics research under the two regeneration systems will be different. With this difference in mind, we will consider the following questions. (1) What is the main function of population genetics theories in managing naturally regenerated populations (NRP)? (2) How much useful information in population genetics theories is available? (3) What more is needed to improve the usefulness of population genetics theory?

Role of population genetics

Quantitative genetics is useful in ARP for two reasons: It offers tree breeders the ability to predict potential genetic gain and means to develop techniques for maximizing genetic gain from the reference population. Because of low level of "genetic" management intensity, it is not possible to study all the NRPs using quantitative genetic techniques. Therefore, in NRP quantitative genetics is no longer the primary means that directly influences management decisions, although it will continue to be useful for some empirical studies. This limited possibility for using quantitative genetic techniques implies that the power of predictions or genetic manipulations in NRPs is much weaker than those in ARPs. Therefore, it is more suitable to say that the research goals in NRPs are to explain potential consequences of management actions and define general management principles. The major source of information for managing NRPs is population biology that encompasses population ecology, silviculture, and population genetics. Population genetics theories influence management decisions in NRPs as a subdiscipline of population biology. As indicated above, the application

of population genetics theories in NRPs will not be as exacting as that of quantitative genetics in ARPs.

Some useful population genetics information:

Basic population genetics theories, especially those dealing with equilibrium properties of populations, are available. These theories can be useful in sorting out different issues in managing NRPs, and defining some guiding principles. In ARPs, we can develop specific prescriptions that would maximize expected economic gains. In NRPs it is not possible to determine such prescriptions. However, by using population genetics theories we can define management activities that may be avoided (limiting conditions). Some recent information that can be used to determine limiting conditions are: Bottleneck effect (Bryant et al. 1986a, b, Maruyama and Fuerst 1984, 1985a, 1985b, Nei et al. 1975), minimum viable population size (Franklin 1980, Lande and Barrowclough 1987), minimum number of migrants to maintain effective panmixia (Slatkin 1985), and protected polymorphism (Gregorius and Namkoong 1983, Namkoong and Gregorius 1985).

Information needed:

Although we can define some limiting conditions, there are two major problems with using population genetics theories to generate management recommendations. (1) Population genetics theories frequently assume away factors that are not directly considered in the investigation. Therefore, if we use a collection of these more or less independent theories to develop management recommendations (limiting conditions) in NRPs, the most conservative measure is likely to dictate the final conclusion. Consequently, it might become impossible to implement the recommendation. We need a way to better unify the limiting conditions. (2) Another common feature of the theories is that they consider the environment to be constant. Therefore, theoretic populations will frequently reach some equilibria. Obviously, natural environments are rarely constant. When ecological factors are superimposed to the population genetics theories, the population may more frequently not move towards equilibria nor obtain equilibria (Namkoong 1988). Theories dealing with such nonequilibrium populations need to be developed. Non-equilibrium theories may be more realistic in concept, but they are more difficult to apply to a particular NRP because theories on transient states do not have as much global meaning as those on equilibria and usually little is known about the actual population.

The value of developing theory on unifying different limiting conditions and non-equilibrium populations will greatly depend on the availability of actual population biological information, such as natural population size and structure, mating system, migration patterns, species interaction etc., even if this information can not be as detailed and specific as that in ARPs. We also need better information on the nature of value functions under different management objectives at different levels such as stand, forest, and region. Without better biological information and some well-defined value functions management recommendations generated from theories may frequently turn out to be too conservative.

SIGNIFICANCE OF AN ARTIFICIAL SELECTION IN A NATURAL POPULATION

A basic question about natural regeneration of forest trees is: Will selective harvesting and regeneration methods seriously influence the genetic properties of naturally regenerated forest tree populations? Traditionally, the answer to this question has been assumed to be "yes". With this assumption, silviculture books (Daniel et al. 1979, Smith, 1962) intuitively described genetic consequences of various reproduction methods. Many forest geneticists also have assumed that an intense selection in natural population could be effective in obtaining genetic gain (Zobel and Talbert 1984, Ledig 1974), and compared efficiencies of using different selection techniques (Ledig 1974). The above geneticists' assumption can be translated into saying that intensive selective harvesting or regeneration methods that leave a small number of extreme individuals could significantly influence the genetic structure of the naturally regenerated populations.

Currently available research results, however, offer mixed conclusions. Pitcher (1982) and Neale (1985) indicated that selective harvesting and/or regeneration methods have little impact on the genetic properties of naturally regenerated populations, while Wilusz and Giertych (1974) and Yazdani et al. (1985) offered the opposite conclusion. Roberds and Conkle (1984) observed in a pair of loblolly pine populations -- parent population and its naturally regenerated progeny population -- that although allele frequencies did not differ, the genetic substructures (F-statistics) differed between successive generations. Given these mixed experimental results, it is useful to examine the basic question again. In this section, I will address this question by using simple algebra available in population genetics.

To facilitate this analysis we need to define the terms "genetic property" and "serious influence." Two parameters -- changes in trait means of populations due to selection, and changes in allele frequencies of the loci influencing the trait -- will be used to represent the term "genetic property". "Seriousness" is a subjective matter. The most convincing definition of "seriousness" would be a statistical significance. In fact, all the above research results used statistical techniques to draw their conclusions. We will also use a fact in evolution, industrial melanism in peppered moth (Biston beturalia), as another means of defining "seriousness" (Hartl 1980). The changes in peppered moth in response to the progressive pollution of the environment by coal soot during the industrial revolution in Manchester, England (Industrial Melanism) is considered to be a dramatic evolutionary change observed. Therefore, if the strength of selection in a NRP turns out to be greater than that observed in Industrial Melanism, we may say that the selection significantly influenced the naturally regenerating populations.

Comparing Statistical Significance (SS) and Industrial Melanism (IM)

Statistical Significance (SS) :--Suppose we chose an extreme (either good or bad) and a random group of individuals from a natural population of forest trees. From these individuals we collected open-pollinated seeds and planted the seedlings in an environment similar to that of the parental population.

Let μ_1, $\bar{Y}_1$, μ_2, and $\bar{Y}_2$ represent true mean and observed mean of selected and random populations, respectively.

[Assumption 1] The parental population and the two progeny populations have equal number (N) and equal estimated variance (σ_p^2).

To test the hypothesis that $\mu_1=\mu_2$, we may use the t-test. Let $R=\bar{Y}_1-\bar{Y}_2$, then

[1] $$t^* = R/(\sigma_p\sqrt{2/N}).$$

To be able to say that μ_1 and μ_2 are significantly different at the specified level of α, the value of t^* must be equal to or greater than that of t found in the table of Student's t distribution, where t represents the abscissa under Student's t distribution corresponding to α, and α represents the proporof the area in one (or both) tail of the distribution. From [1] we can see that the greater the R the greater the t*. To determine the value of R necessary for a statistical significance, we may replace t^* in [1] with t and rearrange [1] so that,

[2] $$R = t\sigma_p\sqrt{2/N}, \text{ or}$$

$$\delta = R/\sigma_p = t\sqrt{2/N}.$$

Assuming a one-tailed test, we can determine t values and corresponding δ for α=0.05 and 0.01 (Table 1). For example, we may say that the difference between the progeny means are significantly different at α=0.05, given N=400 and δ=0.117 (or $R = 0.117\sigma_p$).

Table 1. t-values and standardized distance between two means (δ) for different population size (N) and significance level (α).

	α=0.05		α=0.01	
N	t[1]	δ	t	δ
100	1.661	.235	2.364	.334
200	1.653	.165	2.345	.235
400	1.649	.117	2.336	.165

[1] t-values are determined using the approximation method suggested in Mood et al. (1974).

[Assumption 2] In the subsequent discussion we will assume that N=400 and use δ=0.117 as the necessary distance between the progeny population means for SS.

R, selection intensity (i) and heritability (h^2): It is well known that R can be interpreted as the genetic gain that would have resulted from the selection in the parental population (Falconer 1981). Therefore, R can be written as,

[3] $R = ih^2\sigma_p$, or

$\delta = ih^2$,

where i represents the selection intensity, and
h^2 represents the heritability of the trait in the parental population.

[Assumption 3] m independent additive loci influence the quantitative trait, and that all the loci have the same distance between the two homozygotes (a*) and allele frequency (q) (additive symmetric independent loci).

If m independent additive loci influence a quantitative trait, the additive genetic variance (Hartl 1980):

$$\sigma_A^2 = 2\sum_{i=1}^{m} q_i(1-q_i)a^{*}_i{}^2$$

where $a^{*}_i{}^2$ represents the difference between genotypic values of homozygotes in the i^{th} locus, and q_i represents the allele frequency in the i^{th} locus.

If we let $a_i = a^{*}_i/\sigma_p$, then

$$h^2 = \sigma_A^2 = 2\sum_{i=1}^{m} q_i(1-q_i)a_i^2,$$

because $\sigma_p^2 = 1$ with the normalization.

From Assumption 3, $q_i=q_j=q$ and $a_i=a_j=a$ for all i,j,

$h^2 = 2mq(1-q)a^2$, and

$a = \sqrt{h^2/[2mq(1-q)]}$

[Assumption 4] We further assume that q=0.5.

Then,

[4] $a = \sqrt{2h^2/m}$.

For given values of the average effect (a) and the selection intensity, (i), we can also approximate the selection coefficient (s) (Griffing 1960);

[5] $s \approx ia$,

where the selection coefficient is a component of the fitness in an additive selection model such as:

Genotype	AA	Aa	aa
Fitness	1	1-s/2	1-s

h^2, a, and s for Statistical Significance (when δ=0.117):--By using [3] we can determine the heritability necessary to generate δ=0.117 at different selection intensities (i). Although we assumed that m additive symmetric independent loci are involved in determining the trait expression, we do not know the actual value of m. Therefore, we can not determine "a" and "s." However, it is possible to find "$a\sqrt{m}$" and "$s\sqrt{m}$" from [4] and [5]. For this analysis m=1 will be used because the IM is influenced by a single locus. Table 2 shows values of h^2, a, and s at different "i" for SS when δ=0.117.

Table 2. Heritability, average effect of allele substitution, and Selection coefficients for Statistical Significance when δ=0.117 and for Industrial Melanism*

		Statistical Significance			Industrial Melanism		
p	i	h^2	a	s	h^2	a	s
4/400	2.621	0.045	0.3	0.786	0.003	0.076	0.2
20/400	2.051	0.057	0.338	0.692	0.005	0.098	0.2
40/400	1.749	0.067	0.366	0.64	0.006	0.114	0.2
100/400	1.268	0.092	0.429	0.544	0.012	0.158	0.2
200/400	0.796	0.147	0.542	0.431	0.031	0.251	0.2

* p: Proportion of individuals selected in the natural population. "i" values are taken from Becker (1975).

h^2, a, and s for the Industrial Melanism (IM): --Peppered moth has a single separate generation per year (Hartl 1980). The frequency of melanics among this species increased from approximately 1 percent to 95 percent within 50 years (1848-1898). Hartl (1980) estimated the selection coefficient (s) of IM to be 0.2 by using a single complete dominance locus model. We can determine "a" and h^2 using [4) and [5]. Although the complete dominance model was used in Hartl's estimation, when gene frequency is set to 0.5 as in Assumption 4, the gene frequency change due to selection in this model is the same as that generated from an additive model. Table 2 shows values of h^2 , a, and s at different "i" for Industrial Melanism.

From the third column of the table we can see that values of heritability necessary for SS vary between 0.045 (1% selection) and 0.147 (50% selection). These heritabilities are smaller than those usually found in progeny testings of many forest tree species, but appear to be large enough for breeders to consider selectively breeding for economic gain. Heritabilities of IM (Column 6), however, are substantially smaller (0.003 to 0.031). It is unlikely that a

breeder would wish to do selective breeding for a trait with heritability within this range. Nevertheless, heritabilities in this range would be sufficient to cause an evolutionary change equivalent to that of the IM.

The heritabilities in SS (Column 3) are larger than those of IM (Column 6) by 15 to 4.7 times. By multiplying the heritabilities in Column 6 by corresponding selection intensities (Column 2), we find that δ IM varies between 0.008 and 0.025. Table 4 shows that it does not require large heritability or δ to generate selective force equivalent to IM. Therefore, we can see the danger of trivializing genetic impact of management practices on NRPs because the heritability is low. When we compare s values of SS and IM, we can see that SS is greater than IM by 3.9 to 2.2 times. Therefore, we may say that the selective power of SS is much more potent than that of IM, provided that the assumptions used to derive the conclusion are reasonable. We will examine the assumptions later.

Some examples

black cherry (Prunus serotina): --Pitcher (1982) examined performance of black cherry progenies selected in natural populations. Open-pollinated seeds of trees in three classes (good, average, and poor) were collected in black cherry stands in West Virginia and Pennsylvania, and tested in West Virginia. Although the selection was based on simultaneous consideration of several traits, the analysis of variance showed that at age 12 the impact of selection was significant at α-0.05 with respect to height. However, the selection did not generate significant results for DBH. Table 3 shows the progeny means and the standardized distance between different means using 1.876 as the phenotypic variance (TSS / Total d.f. from Pitcher's (1982) Table 1). Pitcher indicated that the progeny group mean difference between good and average and that between good and poor were statistically not significant. The article did not indicate the actual values of the variances and d.f. used to arrive at the conclusion. If we assume that the experiment was balanced, then the d.f. used in a t-test would be 418, which is close to 400. If we further assume that the variance derived from the TSS (1.876) is a reasonable approximation of the weighted variance used in the t-test then we could use the values in Table 3 as the basis for discussion. From Table 3 we can see that the difference between good and average is statistically not significant at a-0.05, because

Table 3. Means of different black cherry progeny groups and standardized distance between the groups. (σ_p=$\sqrt{1.33}$ is assumed. Data from Pitcher 1982.)

	Mean Height	Standardized Distance		
		Good	Average	Poor
Good	3.98	-	0.1095	0.2847
Average	3.83	-	-	0.1752
Poor	3.59	-	-	-

the standardized distance (0.1095) is less than 0.117, but not too different from 0.117. However, the other two values are substantially larger than 0.117, and must be significant at a-0.05. The difference between good and poor would be significant when N≥100, and that between average and poor would be significant when N≥200 (Table 1). Therefore, although these reconstructed values are not accurate, we could conclude that the difference between the groups must have been fairly close to being significant. We may also say that the selection on tree height in the natural stand of black cherry is more potent than that in IM. This difference is remarkable because tree height was just one of many traits selected simultaneously. Pitcher indicated that diameter growth showed much weaker response to selection than height. This was reflected in the non-significant F ratio (Pitcher's (1982) Table 3). However, no data on means were available for a similar examination.

Scots pine (Pinus silvestris L): --Wilusz and Giertych (1974) examined the impact of silvicultural practices on the genetic quality of Scots pine progeny populations. The experiment was set up by Busse (1924), who collected seeds from populations of different ages in forest district Trzciel in Western Poland and established a progeny test. Wiluz and Giertych assumed that: (1) Trees were thinned in the 19th and 20th centuries according to standard Prussian forestry practices of 19th century, as defined later in Schwappach tables of stocking per ha (Table 4), and (2) the younger populations were descendants of the older populations. However, they did not define potential lineages among them. We will assume that populations with nearest ages represent parent-offspring pairs. For example, individuals in population IIb are assumed to be parents of those in population I. This assumption is conservative because the progeny population mean difference tends to increase as the age difference increases (Table 4). An exception to this trend exists between populations V and VI. The authors suggested that during this period a negative selection for girth had occurred.

Table 4. Mean and standard deviation of DBH in Scots pine progeny populations and standardized distances between populations. (Data from Wilusz and Giertych 1974)

	Population					
Name	I	IIb	III	IV	V	VI
Age	16	47	74	112	140	170
Stocking	9000	2480	928	400	289	210
DBH (Ave.; Cm)	14.3	14.9	14.9	15.3	15.7	15.4
DBH (s.d.)	3.78	3.74	3.69	3.79	4.01	3.85
Stand. Distance*		.159	0	.107	.102	-.763

* Because the authors did not give the number of individuals observed in each population, the average of two standard deviations was used as the pooled s.d. of a pair begin compared. For example, 3.76 was used to to obtain δ for populations of age 16 and 47.

Table 4 shows, in general, that the (absolute) standardized distance between the population means (DBH), when non-zero, are not too different from the δ (-0.117) for SS. They did not measure heights. As was the case with black cherry (Pitcher 1982), the selections for the thinning operations were based on multiple trait considerations. This experiment also leaves a strong impression that silvicultural operations would have much greater influence on genetic changes than IM would.

About the assumptions

Four assumptions were made in the above discussion. I will discuss Assumptions 3 and 4 first. The additive symmetric independent loci assumption was necessary so that simple expression of a (as a function of h^2 and m only) can be defined. If all the allele frequences were the same for all the loci, $a\sqrt{m}$ may be viewed as $\bar{a}\sqrt{m}$, where $\bar{a}=\Sigma a_i/m$. When the allele frequencies of the loci are different, the meaning of "a" is unclear. The assumption that q = 0.5 was made so that an additive model and a complete dominance model could be compared. This analysis compared the force of two selection systems at a given time. No efforts were made to examine the dynamics of the two systems. Therefore, these assumptions represent a state of biological system that is tractable and meaningful as a point of reference.

For most practical purposes, it is reasonable to assume that the size of the natural population to which a silvicultural practice is applied is greater than 400. It is also possible for the size of each progeny group being tested to be 400. However, as Table 1 shows, δ varies greatly depending on N. In many cases $\delta=0.117$ could turn out to be statistically not significant. Therefore, the arbitrary choice of N at 400 ($\delta=0.117$) may appear to lack generality. The main point of this analysis is to demonstrate that if $\delta=0.117$ represents the true standardized distance between two populations, then the selection in the NRP has the properties described in Table 2. This interpretation leads to an alternative approach to examining an observed distance in two progeny populations: (1) Analyze properties of the observed distance in a manner similar to that shown in Table 2, and (2) based on the populations size, N, determine the probability that the observed distance would be true, instead of assigning statistical significance according to $\alpha=0.05$ or 0.01.

The validity of the assumption that σ_p^2 is the same for both parent and progeny population would greatly depend on the species, trait, and age structure of the NRP. For example, Platt et al. (1988) found that the mean and variance in the height of long-leaf pine were not greatly influenced by the ages (say between 60 and 200). Therefore, within this range, not knowing the age distribution of the trees would not inflate σ_p^2 greatly. However, the mean of DBH continued to increase within the same range. In this case σ_p^2 would be inflated if the age structure was ignored. When the phenotypic variance of parent and progeny populations is different, $\delta=ih^2\sigma_{p0}/\sigma_{p1}$, where 0 and 1 indicate parent and progeny populations, respectively. If $\sigma_{p0}>\sigma_{p1}$, then δ would be greater than the case where $\sigma_{p0}=\sigma_{p1}$. However, for a given δ, $\sigma_{p0}>\sigma_{p1}$ means that ih^2 is smaller than that in $\sigma_{p0}=\sigma_{p1}$. In this case the difference between SS and IM would be less than that shown in Table 2.

DETECTION OF ALLELE FREQUENCY CHANGES FROM SELECTION ON QUANTITATIVE CHARACTERS

Suppose we can observe allele frequency changes on all loci influencing a quantitative character through an isoenzyme analysis. If the population before selection is in Hardy-Weinberg equilibrium, then,

Genotype	A_iA_i	A_ia_i	a_ia_i
Fitness	1	$1-s/2$	$1-s$
Frequency	q_i^2	$2q_i(1-q_i)$	$(1-q_i)^2$

After one round of selection from an extremely large population, the new allele frequency in the i^{th} locus is:

$$[6] \qquad q_i' = (q_i[2-s_i(1-q_i)])/(2[1-s_i(1-q_i)])$$

If we sample n alleles from the progeny population, then the expected number of A_i alleles in the sample is Nq_i'. To determine if Nq_i' is significantly different from Nq_i, expected number of A_i alleles in the parent population, we may compare X_i^2 with χ^2 values with 1 degree of freedom, where

$$[7] \qquad X_i^2 = \frac{(Nq_i'-Nq_i)^2}{Nq_i} + \frac{[N(1-q_i')-N(1-q_i)]^2}{N(1-q_i)} = \frac{(q_i'-q_i)^2N}{q_i(1-q_i)}$$

To make the combined test of m loci, we may compare ΣX_i^2 with χ^2 values with m degrees of freedom.

Assume that the quantitative trait is influenced by a single locus, or that we wish to make a single locus test of a multiple loci model and that N-400 and α-0.05. Then, we can determine the minimum value of s necessary to ha e statistically significant changes in allele frequency by equating X with X value at a predetermined level of a with 1 degree of freedom. By combining [6] and [7], and substituting N-400 and q-0.05 we get

$$[8] \qquad X^2 = 100[s/(2-s)]^2 \text{ or}$$

$$s = 2X/(10+X).$$

For α=0.05, χ^2 with 1 d.f. is 3.841. Replacing this value with X^2 in [8] yields s=0.328. If the quantitative trait is influenced by a single locus, then the s values in the 5^{th} column of Table 2 may be compared with 0.328. The smallest value in the 5^{th} column is 0.431, and we conclude that we would probably detect significant allele frequency changes for SS. However, we will not detect significant allele frequency changes in IM.

When m additive symmetric independent loci influence the trait, then we need to determine the per locus selection coefficients. Let Δq represent the expected allele frequency change of a quantitative trait influenced by a single

locus, and let Δq_i represent the expected allele frequency change in i^{th} locus of an equivalent quantitative trait influenced by m loci. Then we can determine s_i by equating,

[9] $\Delta q = \Sigma \Delta q_i$.

When selection is made on an extremely large population, then we may rewrite [9] as,

[10] $\Delta q = m\Delta q_m$, or

$s/[1-s(1-q)] = mS_m/[1-s_m(1-q)]$,

where $\Delta q_i = \Delta q_j = \Delta q_m$, and s_m represents the per locus selection coefficient. From [10] we obtain

[11] $s_m|_{q=0.5} = s/[m-s(m-1)/2]$.

Table 5 shows s_m values for different m when s-0.786 (Column 2). From this table it is evident that we can not observe statistically significant allele frequency changes on the per locus basis when a quantitative trait is influenced by more than three loci. Because 0.786 is the largest value in the Column 5 of Table 2, we conclude that the same is true for all the combinations shown in table 2.

Table 5. Selection coefficients, mX^2, and χ^2 for different number of loci (m).

m	s	mX^2	$\chi^2_{.05(m)}$
1	.786	41.92	3.84
2	.489	20.96	5.99
3	.355	13.97	7.82
4	.279	10.48	9.49
5	.229	8.38	11.07

When the quantitative trait is influenced by multiple loci, we may test the significance of allele frequency changes in all the loci simultaneously by comparing mX_m^2 with $\chi^2_{0.05(m)}$, where X_m^2 is the quantity defined in [8] on the per locus basis. By combining [8] and [11] we get

[12] $mX_m^2 = 100[s/(2-s)]^2/m$.

To examine the properties of multiple loci allele frequency changes we may replace s-0.786 in [12]. Table 5 shows the values of mX^2 and $\chi^2_{.05(m)}$ for different values of m. From the table, it is apparent that for $m \geq 5$, we will not be able to detect the allele frequencies either on the per locus basis or

all the loci combined. From [12] we can see that mX_m^2 is a decreasing function of m, while $X^2.05(m)$ increases as in increases (Table 5). Therefore, even if the selection on a quantitative trait shows the significant difference between two populations, we will not be able to observe significant allele frequency differences if the trait is influenced by five or more additive symmetric independent loci. Because most quantitative traits are likely to have more than five loci, we can draw the following conclusions: (1) The failure to observe statistically significant allele change does not imply that the quantitative trait mean did not change significantly. (2) It would take an extraordinary circumstance to be able to find a significant association between the changes in a quantitative character and that in allele frequency even if allele frequencies can be examined by means of isoenzyme analysis. Therefore, the lack of significant allele frequency change in an NRP such as shown in Neale (1985) should not be interpreted as lack of selection in the silvicultural treatments. Lewontin (1984) thoroughly discussed why detection of statistically significant differences between two populations is much easier with a quantitative character than with allele frequency changes.

CONCLUDING REMARKS

A crude theory was used to compare Satistical Significance and Industrial Melanism, and to examine significant allele frequency changes in a quantitative character. Simplifying assumptions were liberally used in these analyses. Therefore, an attempt to use the results of these analyses to predict the behavior of any real naturally regenerated population (NRP) would be of little value. Despite such shortcomings, these results illustrate the possibly great power of artificial selection. It also shows potential traps in interpreting experimental results. Therefore, despite the lack of precise prediction power this knowledge can certainly help managers in making decisions.

Population genetics theories is available that is more advanced than those developed here. With vigorous application efforts, advanced theory can be made useful in managing NRPs. However, the success in such efforts depends, largely on the availability of basic biological information.

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