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Components of juvenile-mature correlations in forest trees

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Summary. Juvenile-mature correlation has played an important role in indirect selection for size traits in forest trees. The juvenile size of a tree is a part of the mature size, and the juvenile-mature correlation is an example of a "part-whole" type of correlation. As is the case with any other "part-whole" type of correlation, the juvenile-mature correlation can be subdivided into two components; one is a function of variance only, and the other a function of variance and covariance. In this paper the components of the juvenile-mature correlation is described, the basic properties and the dynamics of its components analyzed, and the role of these components in explaining the gain from indirect juvenile selection discussed. Six forest tree populations were used to review the various properties of the model. The most important applied conclusions were: (1) even if two populations have the same juvenile-mature correlations, different selection strategies can be used depending on the nature of correlation components. (2) Choosing the proper mature age is as important as choosing juvenile age. (3) Understanding the growth curves of mean and variance is essential to developing selection strategies.

Key words: Part-whole correlation – Juvenile-mature correlation – Jack pine – Red pine – Norway spruce

1. Introduction

When a genetic correlation exists between two traits, breeders often select for one trait to obtain genetic gain in the correlated character. With mass selection, the gain from indirect selection can be greater than that from direct selection when the heritability (h^2) of the trait selected (x) is greater than that of the correlated trait (y) and the genetic correlation (ϱ) is greater than h_y/h_x (Searle 1965). Even if these conditions are not met, indirect selection is used when direct selection is not possible or is economically less desirable than indirect selection. One such case is juvenile selection in forest trees. By selecting trees at an early age, tree breeders hope to increase the genetic gain per unit time (Dickerson and Hazel 1944) instead of the gain per breeding cycle. By applying this gain-per-unit-time concept to forest tree species, many authors have concluded that selection at early ages is desirable (Nanson 1970; Squillace and Gansel 1974; Franklin 1979; Lambeth 1980; Lambeth et al. 1983; Riemenschneider 1988; Li and McKeand 1989).

Determination of the juvenile selection age at which gain per unit time is maximum can vary greatly depending on the nature of the models used and on their genetic and economic parameters (Kang 1985). Of these parameters, this paper will primarily address the nature of juvenile-mature correlations. Breeders often assume that estimates of genetic correlation (ϱ) exclusively represent expressions of genetic causes – i.e., linkage disequilibrium among loci that influence the two traits, pleiotropic gene action of the loci involved, or both (Falconer 1981). While the estimate of a juvenile-mature correlation of forest tree sizes may indeed reflect these genetic influences, it also includes a component that is a function of variance only (see Eq. [3], Namkoong and Kang 1990). This additional component originates from the fact that juvenile tree size is part of its mature size, and is present in both phenotypic and genetic juvenile-mature correlation coefficients. Because this component is a function of variance only, it does not represent the degree to which two variables (juvenile size and mature size) vary together, and could be

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Annotation: Describes a new way of interpreting juvenile-mature correlation in forest tree species viewed as a factor which inflates the true juvenile-mature correlation. Such terms in correlations have been known to exist whenever the variables have "part-whole" relationship, and these types of correlations have been referred to at times as "spurious correlations" (Sokal and Rohlf 1969).

The presence of this component in the expression of juvenile-mature correlations need not be alarming, because it may not alter past breeding decisions made by tree breeders. However, it is useful to better understand the role of this component. In this paper, I will: (1) present a way of interpreting juvenile-mature correlations by extending the model used in Namkoong and Kang (1990); (2) present a modified expression for genetic gain from indirect selection; and (3) discuss the application of this expression of juvenile-mature correlation by using some examples from forest tree species.

II. Separating variance and covariance in juvenile-mature correlations

In this section I will derive expressions which will allow components of juvenile-mature correlations that are functions of variance only to be separated from those that are functions of both covariance and variance. I will ignore the distinction between phenotypic and genetic correlations until Section IIe, so that the mathematical expressions can be simplified. Lambeth (1980) suggested that genetic juvenile-mature correlations are approximately equal to corresponding phenotypic juvenile-mature correlations in forest trees, and phenotypic correlation may replace genetic correlation in determining the desired selection age. While this may not always be true (Riemenschneider 1988), phenotypic and genetic correlations share essentially the same basic structure. Therefore, the findings of this section will apply to both phenotypic and genetic correlations.

a. Basic expression

Let X_i and X_i' represent sizes of i^{th} individual at time t and $t+\Delta t$, respectively. Also let S_i and S_i' represent standardized variables such that $S_i = X_i/\sqrt{\mathrm{Var}(X_i)}$. Consider the relationship

$$S_i' = S_i + D_i, \tag{1}$$

where D_i represents the difference between S_i' and S_i, and Δt represents an arbitrary period. Then,

$$\mathrm{Cov}(S, S') = \mathrm{Cov}(S, S+D) = V(S) + \mathrm{Cov}(S, D), \tag{2}$$

and

$$r_{SS'} = \sqrt{V(S)}/\sqrt{V(S')} + \mathrm{Cov}(S, D)/[\sqrt{V(S)}\,\sqrt{V(S')}],$$

where V(.) represents Var(.).

Because of the standardization, V(S') equals 1, and

$$r_{SS'} = \sqrt{V(S)} + \mathrm{Cov}(S, D)/\sqrt{V(S)} = \sqrt{V(S)} + C(S, D), \tag{3}$$

as shown in Namkoong and Kang (1990). From this identity, we can see that a correlation coefficient of a size between time t and $t+\Delta t$ is a function of two components, $\sqrt{V(S)}$, and $C(S, D)$ $(= \mathrm{Cov}(S, D)/\sqrt{V(S)})$. Based on this expression, it is possible to conclude that $\sqrt{V(S)}$ is an inconsequential component of the correlation coefficient because a variance is a parameter associated with a single variable. We may also argue that traditional estimation of juvenile-mature correlation is not a useful measure, and that we must use the correlation coefficient between juvenile size and subsequent growth, $r_{SD} = \mathrm{Cov}(S, D)/[\sqrt{V(S)}\,\sqrt{V(D)}]$, as an alternative measure. However, the presence of $\sqrt{V(S)}$ in (3) does not necessarily imply that calculating and using correlation coefficients between variables with "part-whole" relations are of little value (Sokal and Rohlf 1969). This point will become clearer when we examine the expression of genetic gain from selection in Section IIe.

b. Alternate expressions

If S and D are variables such that one cannot be expressed as a function of the other, then Cov(S, D) cannot be reduced any further. For tree sizes, however, the second term in (3), C(S, D), may be further subdivided into two subcomponents, where one is a function of variance and the other a function of covariance and variance. This is done by expressing D in (1) in terms of relative growth (δ_i) of an individual (i) between time t and $t+\Delta t$ and the size (S) at time t. Therefore, from (1)

$$S_i' = S_i + \delta_i S_i = S_i + (\alpha + \beta_i) S_i, \tag{4}$$

where

$$\delta_i = D_i/S_i,$$

$$\alpha = \left(\sum_{i=1}^{N} \delta_i\right)/N,$$

$$\beta_i = \delta_i - \alpha,$$

and

N = the number of individuals in the population.

From (2)

$$\begin{aligned}\mathrm{Cov}(S, S') &= V(S) + \mathrm{Cov}[S, (\alpha+\beta) S] \\ &= V(S) + \alpha V(S) + \mathrm{Cov}(S, \beta S),\end{aligned}$$

and

$$r_{SS'} = \sqrt{V(S)} + \alpha\sqrt{V(S)} + \mathrm{Cov}(S, \beta S)/\sqrt{V(S)} \tag{5}$$

$$r_{SS'} = (1+\alpha)\sqrt{V(S)} + C(\beta). \tag{6}$$

In (5), the first term is entirely due to the standard deviation of the size at time t. The second term is a function of α and $\sqrt{V(S)}$. In this paper α will be referred to as the mean relative growth. The term "relative" is used here because the growth (D) of an individual between time t and $t+\Delta t$ is divided by the size (S) at time t. The β in (5) represents the deviation in relative growth of individuals from α. The second term in (6), $C(\beta)\,(=\mathrm{Cov}(S, \beta S)/\sqrt{V(S)})$, can be further subdivided if we know the substructure of the populations, such as family, block, etc. However, all such subdivisions produce components that are functions of both variance and covariance (Appendix A).

c. Basic properties of the alternate expressions

Equations (3) and (5) are equivalent. If the same data set is analyzed using different models, the resulting $r_{SS'}$ will be the same, and

$$\mathrm{Cov}(S, D) = \alpha\, V(S) + \mathrm{Cov}(S, \beta S).$$

If we assume that $C(\beta)=0$ in (6), then

$$r_{SS'} = (1+\alpha)\sqrt{V(S)}. \tag{7}$$

If we further assume that the zero covariance originates from zero deviations – i.e., $\beta_i=0$ for all i – then, from (4),

$$S'_i = (1+\alpha)\, S_i,$$

and

$$\begin{aligned} V(S') &= (1+\alpha)^2\, V(S) \qquad (8)\\ &= r^2_{SS'} \text{ (from (7))}\\ &= 1, \text{ because we standardized the variance such that } V(S')=1. \end{aligned}$$

Equivalently,

$$\sqrt{V(S)} = 1/(1+\alpha).$$

These identities imply that when all the individuals increase their sizes exactly α times their original sizes, the correlation coefficient must equal to unity for all t, and the variance at time $t+\Delta t$ must be $(1+\alpha)^2$ times that at time t.

There are circumstances under which $r_{SS'}=1$, even if $\mathrm{Cov}(S, \beta S) \neq 0$. For example, when $S'_i = S_i + K$ for all i, where K is a constant, then $\sqrt{V(S)} = \sqrt{V(S')} = 1$, and $\alpha = -C(\beta)$ will result in $r_{SS'}=1$.

When $\beta_i \neq 0$ for some i, not all individuals increase their sizes α times their original sizes and an imperfect correlation results because $\mathrm{Cov}(S, \beta S) \neq 0$ for most situations. It is possible to have $\mathrm{Cov}(S, \beta S)=0$, even if $\beta_i \neq 0$ for some i, when the sum of the cross products of S and βS equals zero. This situation may not arise frequently in actual populations. It will be shown at the end of the next paragraph that all β_i must equal zero when $V(S') = (1+\alpha)^2\, V(S)$ and $\mathrm{Cov}(S, \beta S)=0$.

If all $\beta_i \neq 0$, but $V(S') = (1+\alpha)^2\, V(S)$, then $\mathrm{Cov}(S, \beta S)$ cannot be greater than zero. From (1),

$$\begin{aligned} V(S') &= V(S) + V(D) + 2\,\mathrm{Cov}(S, D)\\ &= (1+\alpha)^2\, V(S) + V(\beta S) + 2(1+\alpha)\,\mathrm{Cov}(S, \beta S),\\ &= V(S') + V(\beta S) + 2(1+\alpha)\,\mathrm{Cov}(S, \beta S), \qquad (9) \end{aligned}$$

and

$$V(\beta S) = -2(1+\alpha)\,\mathrm{Cov}(S, \beta S). \tag{10}$$

From (10) we see that $\mathrm{Cov}(S, \beta S) \leq 0$, because $\alpha > 0$ and $V(\beta S) \geq 0$. Thus, $\mathrm{Cov}(S, \beta S)$ can never be positive when $V(S') = (1+\alpha)^2\, V(S)$. Furthermore, it is not essential to have $\mathrm{Cov}(S, \beta S)=0$ to obtain the identity $V(S') = (1+\alpha)^2\, V(S)$. As long as $\mathrm{Cov}(S, \beta S)$ satisfies (10), Eq. (9) will reduce to (8). Equation (10) also indicates that if $\mathrm{Cov}(S, \beta S)=0$, then $V(\beta S)=0$. Thus, unless $S_i = S_j = S$ for all i and j, $V(S') = (1+\alpha)^2\, V(S)$ and $\mathrm{Cov}(S, \beta S)=0$ requiring that $\beta_i = 0$ for all i. This proves the last point made in the previous paragraph.

We also need to consider the case where $r_{SS'} \neq (1+\alpha)\sqrt{V(S)}$. From (6),

$$r_{SS'} = (1+\alpha)\sqrt{V(S)} + C(\beta).$$

If $r_{SS'} < (1+\alpha)\sqrt{V(S)}$, then $C(\beta) > 0$, and $\mathrm{Cov}(S, \beta S) > 0$, and if $r_{SS'} > (1+\alpha)\sqrt{V(S)}$, then $C(\beta) > 0$, and $\mathrm{Cov}(S, \beta S) > 0$. Because $r_{SS'} \leq 1$, a necessary but not sufficient condition for a positive $C(\beta)$ is

$$\sqrt{V(S)} < 1/(1+\alpha), \text{ which means } V(S') > (1+\alpha)^2\, V(S). \tag{11}$$

On the other hand,

$$\sqrt{V(S)} > 1/(1+\alpha), \text{ or } V(S') < (1+\alpha)^2\, V(S) \tag{12}$$

is sufficient for $C(\beta) < 0$. Equation (12) also implies that $(1+\alpha)\sqrt{V(S)} > 1$, and that $|C(\beta)| > 1 - r_{SS'}$. It can be readily shown that $1+\alpha$ is the arithmetic mean of S'_i/S_i $(=\mu(S'/S))$, and that $1/(1+\alpha)$ is the harmonic mean of $S_i/S'_i\,(=\mu_h(S/S'))$. We may, then, replace $1/(1+\alpha)$ in (11) and (12) with $\mu_h(S/S')$. Therefore, simply by comparing $\sqrt{V(S)}$ at time t to the harmonic mean of S_i/S'_i we can often predict the sign of $\mathrm{Cov}(S, \beta S)$ (or the sum of covariances in (23) in Appendix A).

The basic mathematical properties of the alternate expressions of $r_{SS'}$ (Eqs. (5) and (6)) offer some points to consider. First, if all the trees grow exactly α times their initial sizes, the correlation coefficient would always be unity, and would be a function of the relative growth and variance at juvenile stage only $(r_{SS'} = (1+\alpha)\sqrt{V(S)})$. Although intuitively obvious, this identity is a useful reference which defines the condition under which the correlation coefficient can be expressed without involving any covariance terms. Under this condition, $C(\beta)=0$.

Second, we can view imperfect correlations as indicating that trees failed to grow exactly α times their original sizes. This inability produces non-zero (mostly negative)

$C(\beta)$. The negative $C(\beta)$ means that $\sqrt{V(S)}$ is greater than the harmonic mean of S/S'. In many real situations, the difference (λ) between arithmetic mean and harmonic mean is small, and we may conveniently think that when $\sqrt{V(S)}$ is greater than the arithmetic mean of S_i/S_i' then $C(\beta)$ will be negative.

Third, the variance usually does not increase fast enough to meet the condition $V(S') > (1+\alpha)^2\,V(S)$ (Section III). A potential cause for this is that the relative growth (δ) of larger juvenile trees are less than α ($\beta_{\text{large}} < 0$), while those of smaller trees are greater than α ($\beta_{\text{small}} > 0$). When this is true, the responses to selection will tend to be less than those predicted from the correlation coefficients in a directional selection.

Fourth, the fact that $C(\beta) < 0$ when $\sqrt{V(S)} > 1/(1+\alpha)$ (or $\mu_h(S/S')$) also suggests that it is critical to carefully define the desired mature age as well as the juvenile age. For example, if we ignore economic considerations, we may define the best mature age as the time at or beyond a certain predetermined age when the size variance is maximum. We may then define the desired juvenile age as the time when the ratio $\alpha/\sqrt{V(S)}$ is minimum.

d. Changes in the components of Equations [3] and [5] with age

As trees increase in size, the size variance tends to increase. In the past, this increase was not considered useful in understanding juvenile-mature correlations; it was not necessary to have a measure to compare the increase in the variance. The new expressions of correlation coefficients and related functions (Eqs. [3] through [12]) offer a means of connecting mean relative growth (α), $\sqrt{V(S)}$ and the correlation coefficient. Therefore, it is worthwhile examining how various components of the expression of correlation coefficients change with age.

Suppose tree sizes are measured at different ages and that the correlation coefficients are determined between size at T and that for all other ages (t), where T represents the oldest (or mature) age. Namkoong and Kang (1990) indicated that the correlation coefficient will increase with age primarily due to the increase in $\sqrt{V(S)}$. If this is true, tree populations at similar stages of growth with similar relative rates of increase in mean and variance of size are likely to display similar patterns of increase in juvenile-mature correlations. This would be true even among species, and can explain why Lambeth's (1980) equation appears to apply well to many species in *Pinaceae*. In this section I will develop mathematical arguments defining circumstances when the assertion by Namkoong and Kang (1990) is true.

Changes in the correlation coefficients of size with age reflect biological phenomena, and we cannot develop mathematical rules which could explain all the changes. However, two biological properties can be used to mathematically examine the changes of the components in [3] and [5]: $\sqrt{V(S)}$, which tends to increase with age, and α, which tends to decrease with age.

In [5], there are three components, all of which are functions of $\sqrt{V(S)}$. Although it is not always true that $\sqrt{V(S)}$ increases with age (see red pine example in Section III), we may generally assume that $\sqrt{V(S)}$ increases with age and that $\sqrt{V(S)} \le 1$. Then, we are primarily interested in knowing how $\alpha\sqrt{V(S)}$, $C(\beta)$ $(=\mathrm{Cov}(S, \beta S)/\sqrt{V(S)})$, and $C(S, D)$ $(=\mathrm{Cov}(S, D)/\sqrt{V(S)} = \alpha\sqrt{V(S)} + C(\beta))$ change with time. Let

$$\sqrt{V(S)} = [1/(1+\alpha)] + d,$$

where

$$-1/(1+\alpha) \le d \le 1 - [1/(1+\alpha)]. \tag{13}$$

Then,

$$\alpha\sqrt{V(S)} = [\alpha/(1+\alpha)] + d\alpha. \tag{14}$$

From [14], we can see that $\alpha/(1+\alpha)$ decreases as α decreases. The change in $d\alpha$ depends on the changes of d. If d decreases or is constant, $d\alpha$ decreases as α decreases. When d increases, we cannot predict the behavior of $d\alpha$. We can only make a conditional statement that $\alpha\sqrt{V(S)}$ decreases as long as d does not increase with age.

Changes in the domain of d with age is more predictable. The width of the domain of d $[-1/(1+\alpha), 1-1/(1+\alpha)]$ is always 1 and is a function of α only. Because α decreases with age, d shifts from the right to the left of the real line. For example, if $\alpha = 19$, then, $-0.05 \le d \le 0.95$; but if $\alpha = 0$, then $-1 \le d \le 0$. During early juvenile stages, when α is large, the wider portion of the domain lies on the positive side of the real line, and $\sqrt{V(S)}$ will tend to be greater than $1/(1+\alpha)$ (or $V(S') < (1+\alpha)^2\,V(S)$). As t increases, α decreases and the domain moves to the left.

If we assume that the pattern of change in d follows that of its domain, then $\alpha\sqrt{V(S)}$ was found to decrease with age in all forest tree examples (Section III).

The denominator of $C(\beta)$ increases with t. Therefore, if the absolute value of the numerator does not increase as fast as (or faster than) the denominator, the absolute value of $C(\beta)$ will decrease. If the sign of $\mathrm{Cov}(S, \beta S)$ is initially negative, then this decrease in absolute value means an increase in the actual value of $C(\beta)$. As shown in Eqs. (11) and (12), the sign of $\mathrm{Cov}(S, \beta S)$ depends on d. The sufficient condition for $\mathrm{Cov}(S, \beta S) < 0$ is $\sqrt{V(S)} > 1/(1+\alpha)$, but this also implies that $d > 0$. Since the domain of d is mostly positive for large α, $\mathrm{Cov}(S, \beta S)$ is likely to be negative at early ages. As the domain moves to the left with age, $\mathrm{Cov}(S, \beta S)$ will become less negative – i.e., the absolute value of $\mathrm{Cov}(S, \beta S)$ will decrease as long as the sign remains the same. Therefore, assuming that $\sqrt{V(S)}$ does not drastically shift around $1/(1+\alpha)$, $C(\beta)$ will tend to increase with time.

In most applied situations, $\alpha\sqrt{V(S)}$ is positive and tends to decrease, while $C(\beta)$ is negative and tends to increase with t. However, we do not know the relative magnitudes of these terms, and it is difficult to determine how the sign and magnitude of $C(S, D)$ $(=\mathrm{Cov}(S, D)/\sqrt{V(S)})$ in (3) changes with age. If $C(S, D)$ was positive at the early ages, then it is likely to become smaller, because absolute values of $\alpha\sqrt{V(S)}$ and $C(\beta)$ tend to decrease. $\mathrm{Cov}(S, D)$ will often remain positive because the shift of the domain of d to the left will tend to move $\mathrm{Cov}(S, \beta S)$ toward the positive side (Eq. (12)). Therefore, if $C(S, D)$ were initially positive, it is likely to be reduced, especially near mature age, and $\sqrt{V(S)}$ will be the only component of the correlation coefficient in Eq. (3) which increases with age (Namkoong and Kang 1990).

If $C(S, D)$ was negative at an earlier age, it will move toward the positive side of the real line, because $\mathrm{Cov}(S, \beta S)$ will become less negative or positive with increasing t. Therefore, $C(S, D)$ as well as $\sqrt{V(S)}$ increases with age. In this case we do not know which of the two components in (3) increases more rapidly with time.

e. Genetic gain from juvenile selection

As stated in Section II a, the presence of $\sqrt{V(S)}$ in the expression of a juvenile-mature correlation (Eq. (3)) does not imply calculating and using the correlation $r_{ss'}$ is of little value. This statement can be made clearer when we examine the expression for genetic gain from indirect selection. We may define the expressions of the genetic correlation coefficient by rewriting (3) and (6) such that

$$\varrho_{ss'} = \sigma_s + c(s, d) \qquad (15)$$

$$= (1+\alpha)\,\sigma_s + c(\beta), \qquad (16)$$

where

$\varrho_{ss'}$ = genetic correlation coefficient,
σ_s = standardized additive genetic variance of the trait at $t\,(\sigma_{s'}=1)$,
$c(s, d) = \mathrm{cov}(s, d)/\sigma_s$,
$c(\beta) = \mathrm{cov}(s, \beta s)/\sigma_s$,
cov(.) represents genetic covariance, and
α is assumed to be the same for both genetic and phenotypic values.

The gain at T when selection is made at t is (Falconer 1981):

$$\Delta G_{T|t} = i\,h_s\,h_{s'}\,\varrho_{ss'}\sqrt{V(S')}, \qquad (17)$$

where h^2 represents heritability, and i represents selection intensity. Note that $\sigma_{s'}=1$, but $\sqrt{V(S')}$ does not necessarily equal unity because the phenotypic standard deviation at T is divided by the genetic standard deviation at T. By substituting $\varrho_{ss'}$ in (17) with (15) and noting that $\sigma_{s'}=1$,

$$\Delta G_{T|t} = i\,h_s\,h_{s'}\,[\sigma_s + \mathrm{cov}(s, d)/\sigma_s]\sqrt{V(S')}$$

$$= i\,h_s\,\sigma_s[1 + \mathrm{cov}(s, d)/\sigma_s^2]$$

$$= G_t + [\mathrm{cov}(s, d)/\sigma_s^2]\,\Delta G_t. \qquad (18)$$

Equation (18) shows the composition of the overall gain from juvenile selection in [17]. The first part, ΔG_t, represents the gain one would expect from direct selection on the juvenile size alone. This gain is entirely due to the presence of σ_s in $\varrho_{ss'}$ (Eq. (15)), and would occur regardless of the rankings or performances of juvenile-selected individuals at the mature age. Therefore, σ_s in (15) is an important integral component of $\varrho_{ss'}$. The second part of (18), $[\mathrm{cov}(s, d)/\sigma_s^2]\,\Delta G_t$, represents the additional gain due to the covariance between the juvenile size and subsequent growth. This additional gain comes from the performance or ranking of the juvenile selected individuals at the mature age.

Equation (18) also indicates that for a given $\varrho_{ss'}$, different combinations of σ_s and $c(s, d)$ can exist. Consequently, even if the overall gain is the same, the nature of genetic gain from an indirect selection could vary depending on the relative magnitudes of the above two components. For example, when σ_s is much greater than $c(s, d)$, as is the case when the selection age is close to the mature age, the gain comes primarily from ΔG_t, while the opposite is true when σ_s is small compared with $c(s, d)$.

Since $\mathrm{cov}(s, d) = \alpha\,\sigma_s^2 + \mathrm{cov}(s, \beta s)$,

$$\Delta G_{T|t} = \{1 + [\alpha\,\sigma_s^2 + \mathrm{cov}(s, \beta s)]/\sigma_s^2\}\,\Delta G_t$$

$$= [(1+\alpha) + \mathrm{cov}(s, \beta s)/\sigma_s^2]\,\Delta G_t. \qquad (19)$$

The genetic gain expression in (19) is more informative than the traditional expression of the gain. When $\mathrm{cov}(s, \beta s)$ is zero, the gain at T is exactly $(1+\alpha)$ times that at t, which is equal to that from direct selection at T – i.e., $\Delta G_{T|t} = \Delta G_T$. When $\alpha = 0$ in addition to $\mathrm{cov}(s, \beta s) = 0$, the gain equals that at juvenile selection. In most cases, the gain will fall somewhere between ΔG_t and $(1+\alpha)\,\Delta G_t$, because $\mathrm{cov}(s, \beta s)$ is likely to be negative.

If $\sigma_s < 1/(1+\alpha)$, or $V_{s'} > (1+\alpha)^2\,V(s)$, the chance of having positive $\mathrm{cov}(s, \beta s)$ increases (Eq. (19)), and it is possible to have a genetic gain that is greater than that obtained by selection at the mature stage. The presence of positive $\mathrm{cov}(s, \beta s)$ implies that $\varrho_{ss'} > h_{s'}/h_s$, the condition mentioned in the Introduction (Searle 1965). To see this, we divide both sides of Eq. (17) with ΔG_T to obtain,

$$\Delta G_{T|t}/\Delta G_T = \varrho_{ss'}\,(h_s/h_{s'}). \qquad (20)$$

Using the expression in (19) we find that

$$\Delta G_{T|t}/\Delta G_T = \{(1+\alpha)\,\Delta G_t + [\mathrm{cov}(s, \beta s)/\sigma_s^2]\,\Delta G_t\}/\Delta G_T$$

$$= 1 + [\mathrm{cov}(s, \beta s)/\sigma_s^2]\,(\Delta G_t/\Delta G_T)$$

$$= 1 + [\mathrm{cov}(s, \beta s)/\sigma_s^2]\,(i\,h_s\,\sigma_s/i\,h_{s'}\,\sigma_{s'}) \qquad (21)$$

$$= 1 + [\mathrm{cov}(s, \beta s)/\sigma_s]\,(h_s/h_{s'}),\ \text{because}\ \sigma_{s'} = 1.$$

By equating (20) and (21)

$\varrho_{ss'}(h_s/h_{s'}) = 1 + (\mathrm{cov}(s, \beta s)/\sigma_s)(h_s/h_{s'})$, and

$\varrho_{ss'} = h_{s'}/h_s + \mathrm{cov}(s, \beta s)/\sigma_s$.

Therefore, $\mathrm{cov}(s, \beta s) > 0$ automatically implies that $\varrho_{ss'} > h_{s'}/h_s$, which is the necessary condition for $\Delta G_{T|t}/\Delta G_T > 1$ (Searle 1965).

III. Forest tree examples

Six populations of three species, jack pine (JP, JO), red pine (RC, RS9, RS11), and Norway spruce (NS), are used to show components of juvenile-mature correlations, and to further discuss various points made in Section II. The basic information on the data sets is included in Appendix B. Multiple-year height measurements were obtained from the above six populations. Individuals with scores missing for some years or with scores at earlier ages greater than those at later ages were deleted from the data sets.

Only phenotypic correlations are used in these examples. Separate analyses will be needed to more thoroughly examine these populations. It is possible, however, to discuss genetic selection strategies using the examples of phenotypic correlations.

Table 1. Annual growth rate ($\bar{S}_T/T$), coefficient of variation (CV) at T, and $d(=\sqrt{V(S)} - 1/(1+\alpha))$ at the youngest age

	$\bar{S}_T/T$	CV	d
JP	0.34	0.17	0.02
JO	0.53	0.11	0.04
NS	0.23	0.27	0.07
RC	0.46	0.03	0.24
RS9	0.50	0.05	0.30
RS11	0.50	0.05	0.38

a. Height growth, mean growth rate, and relative height

Mean height of all the populations continued to increase, and there was no indication that growth reached a plateau during the periods observed (Fig. 1). Jack pine and Norway spruce populations were much younger than red pine populations. The mean annual growth rate ($\bar{S}_T/T$) of JO was greatest, while that for NS was smallest (Table 1). The annual growth rates of the two jack pine populations (JP and JO) appeared to increase with age, while those of Norway spruce were more constant (Fig. 1a). The annual growth rate of RC appeared to decrease with age, in three different stages (Fig. 1b). Thus, although the actual growth of RC up to age 23 was greater than that of RS9 or RS11 (Fig. 1b), the mean growth rate of RC (0.46) was smaller than that of RS9 or RS11 (0.5).

The harmonic means ($\mu_h(S/S') = 1/(1+\alpha)$) of height ratio show essentially the same trends as the mean heights (Fig. 2). The differences (λ) between arithmetic means and harmonic means of the height are small (less than 0.015) for all populations (Table 2, last column). Therefore, the harmonic mean and the arithmetic mean can be interchanged without greatly influencing the results.

b. Variance

In jack pine and Norway spruce the ratio of standard deviations ($\sqrt{V(S)}$) monotonically increased, while in red pine $\sqrt{V(S)}$ changed irregularly (Fig. 2, Table 2 column 5). At the youngest ages for jack pine and Norway spruce,

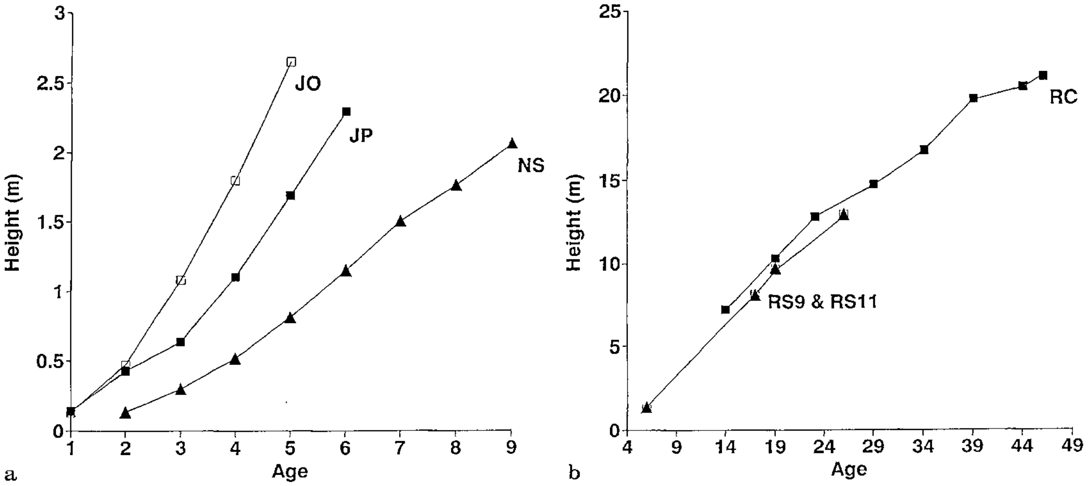

Fig. 1 a, b. Height growth in the six populations. **a** Jack pine and Norway spruce. *JP* Jack pine parent population, *JO* jack pine offspring population, *NS* Norway spruce. **b** Red pine. *RC* Red pine at Chippewa, *RS9* red pine at Spooner with 9′ × 9′ spacing, *RS11* red pine at Spooner with 11′ × 11′ spacing

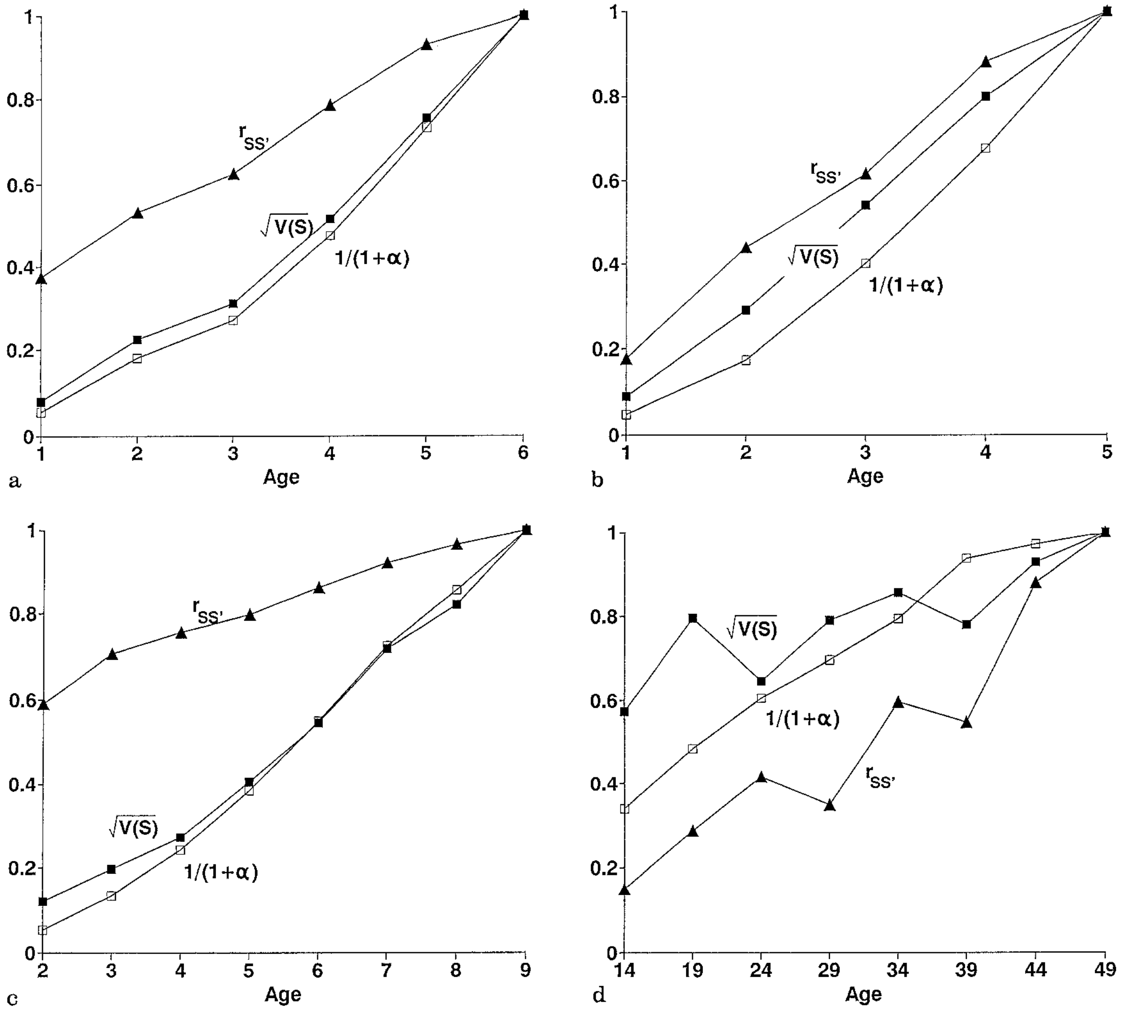

Fig. 2a–d. Relative means and standard deviations of tree sizes with age. **a** Jack pine parent population (*JP*); **b** jack pine offspring population (*JO*); **c** Norway spruce (*NS*); **d** red pine at Chippewa (*RC*)

$\sqrt{V(S)}$ was much smaller than for red pine populations (Table 2, Fig. 2). This does not imply that red pine is in general more variable than other species. The coefficients of variation (CV) at the oldest age in the red pine populations were much smaller than those in other species, and the large initial $\sqrt{V(S)}$ suggests that the variances of red pine do not increase with age as much as those in other species. In fact, $\sqrt{V(S)}$ of RC at age 19 was greater than that for many older ages, and $\sqrt{V(S)}$ exceeded 1 for ages 17 and 19 in RS11 (Table 2). It could be argued that such large juvenile variance in red pine could be due to the older ages when the trees were first measured. If this is the case, we would expect the magnitudes of $d(=\sqrt{V(S)}-1/(1+\alpha))$ for red pine to be similar to those for other species. Table 1 shows that the d (Equation (13)) values at the youngest ages of red pine are at least three times as large as those for other species. Therefore, we can conclude that $\sqrt{V(S)}$ in red pine is much greater than that expected based on the harmonic mean of S/S′ alone.

c. Changes in $\alpha\sqrt{V(S)}$, $C(\beta)$, and d

Although patterns of change in $\sqrt{V(S)}$ among the populations differed, $\alpha\sqrt{V(S)}$ and the absolute values of $C(\beta)$ decreased with age for all the populations. This implies that either d decreased or the changes in d were not strong enough to offset the decrease in α and $\alpha/(1+\alpha)$, or both (Eq. (14)). Indeed, d was positive for all the populations during the early ages. The value of d subsequently decreased, although not strictly monotonically, with age (Fig. 2). The presence of positive d means that $\mathrm{Cov}(S, \beta S)<0$ (Eq. (12)). $C(\beta)$ was less than zero for all the populations at early ages (Table 2, column 8). In NS and RC, d values became negative at older ages. Negative d was shown at ages 7 and 8 for NS and ages 39 and 44 for RC. The negative d satisfies the necessary but not sufficient condition for positive $\mathrm{Cov}(S, \beta S)$ (Eq. (11)). The positive $C(\beta)$ was shown only at age 8 for NS.

Table 2. Components of juvenile-mature correlations

	t	T	$r_{SS'}$	$\sqrt{V(S)}$	C(S, D)	$\alpha\sqrt{V(S)}$	C(β)	α	λ
Jack pine: Parent (N=1,342)	1	6	0.3732	0.0792	0.2939	1.3578	−1.0639	17.1366	0.0042
	2	6	0.5342	0.2235	0.3107	1.0283	−0.7176	4.6008	0.0081
	3	6	0.6267	0.3107	0.3160	0.8441	−0.5281	2.7169	0.0082
	4	6	0.7849	0.5171	0.2678	0.5704	−0.3026	1.1031	0.0077
	5	6	0.9310	0.7539	0.1772	0.2764	−0.0992	0.3666	0.0036
	5	6	1	1	0	0	0	0	0
Jack pine: Offspring (N=1,683)	1	5	0.1769	0.0881	0.0888	1.7926	−1.7038	20.3429	0.0025
	2	5	0.4404	0.2899	0.1505	1.3877	−1.2372	4.7868	0.0054
	3	5	0.6162	0.5418	0.0744	0.8043	−0.7299	1.4846	0.0063
	4	5	0.8801	0.8012	0.0790	0.3839	−0.3050	0.4792	0.003
	5	5	1	1	0	0	0	0	0
Norway spruce (N=798)	2	9	0.5908	0.1195	0.4713	2.1139	−1.6426	17.6875	0.0096
	3	9	0.7069	0.1961	0.5108	1.2809	−0.7701	6.5321	0.0107
	4	9	0.7583	0.2727	0.4857	0.8517	−0.3660	3.1235	0.0105
	5	9	0.7996	0.4060	0.3936	0.6505	−0.2570	1.6022	0.0127
	6	9	0.8627	0.5469	0.3158	0.4476	−0.1318	0.8184	0.0117
	7	9	0.9205	0.7183	0.2022	0.2718	−0.0698	0.3785	0.0085
	8	9	0.9651	0.8211	0.1440	0.1388	0.0052	0.1690	0.0043
	9	9	1	1	0	0	0	0	0
Red pine: Chippewa (N=36)	14	46	0.1498	0.5732	−0.4232	1.1170	−1.5403	1.9488	0.0010
	19	46	0.2877	0.7972	−0.5095	0.8410	−1.3504	1.0549	0.0012
	23	46	0.4171	0.6468	−0.2298	0.4208	−0.6505	0.6505	0.0007
	29	46	0.3494	0.7906	−0.4413	0.3438	−0.7951	0.4348	0.0009
	34	46	0.5965	0.8554	−0.2590	0.2201	−0.4791	0.2573	0.0006
	39	46	0.5473	0.7793	−0.2321	0.0531	−0.2853	0.0682	0.0007
	44	46	0.8778	0.9269	−0.0492	0.0268	−0.0760	0.0289	0.0002
	46	46	1	1	0	0	0	0	0
Red pine: Sp09 (N=80)	6	26	0.3481	0.4039	−0.0558	3.6476	−3.7034	9.0318	0.0047
	17	26	0.6969	0.9598	−0.2629	0.5791	−0.8420	0.6034	0.0022
	19	26	0.6283	0.9811	−0.3528	0.3275	−0.6803	0.3338	0.0023
	26	26	1	1	0	0	0	0	0
Red pine: Sp11 (N=35)	6	26	0.4621	0.5592	−0.0971	5.9224	−6.0195	10.5906	0.0109
	17	26	0.7756	1.1518	−0.3762	0.6914	−1.0676	0.6003	0.0027
	19	26	0.7959	1.0970	−0.3010	0.3772	−0.0782	0.3438	0.0018
	26	26	1	1	0	0	0	0	0

S, Size at a juvenile age (t); T, mature age; N, total number of individuals; $r_{SS'}$, J-M correlation; $\sqrt{V(S)}$, relative standard deviation of size at t; α, mean relative growth rate; C(S, D), Cov(S, D)/$\sqrt{V(S)}$; C(β), Cov(S, β S)/$\sqrt{V(S)}$; λ, $\mu(S/S')-\mu_h(S/S')$

d. A cause for $\sqrt{V(S)} > 1/(1+\alpha)$

A positive d also means that the variance of size at an older age did not increase as much as $(1+\alpha)^2$ – i.e., $V(S') < (1+\alpha)^2\,V(S)$, or equivalently $\sqrt{V(S)} > 1/(1+\alpha)$ (or $\mu_h(S/S')$). It was speculated at the end of Section IIc that a cause for slow increase in variance relative to size increase was that the relative growth rates (δ) of larger juvenile trees were less than $\alpha(\beta_{large} < 0)$ while δ of smaller trees were greater than $\alpha(\beta_{small} > 0)$.

In jack pine and Norway spruce, tree heights at juvenile age were sorted in decreasing order, and the sorted data sets subdivided into 20 groups. In each group the mean of β was obtained and plotted against the group rank, where smaller numbers represent higher ranking groups (Fig. 3a–c). In the red pine populations individual values were used directly, without forming groups, because the total number was small (N=36, Fig. 3d).

From jack pine and early juvenile stages of Norway spruce (t=2) and red pine (t=14), we can clearly see that β (or $\bar{\beta}$) is less than zero for taller juvenile trees, while the opposite holds for shorter trees. The curves for t=8 in Norway spruce and t=44 in red pine show that β values are fairly evenly distributed around zero. In both cases, d<0. Cov(S, β S) for Norway spruce is greater than zero and for red pine less than zero, but Cov(S, β S) are small. The trends of β in RS9 and RS11 (not shown) are similar to that in RC.

From these observations, we may conclude that when d>0 with large negative C(β), deviations from α in extreme individuals are likely to be greater than those in individuals in the middle, and that these situations occur

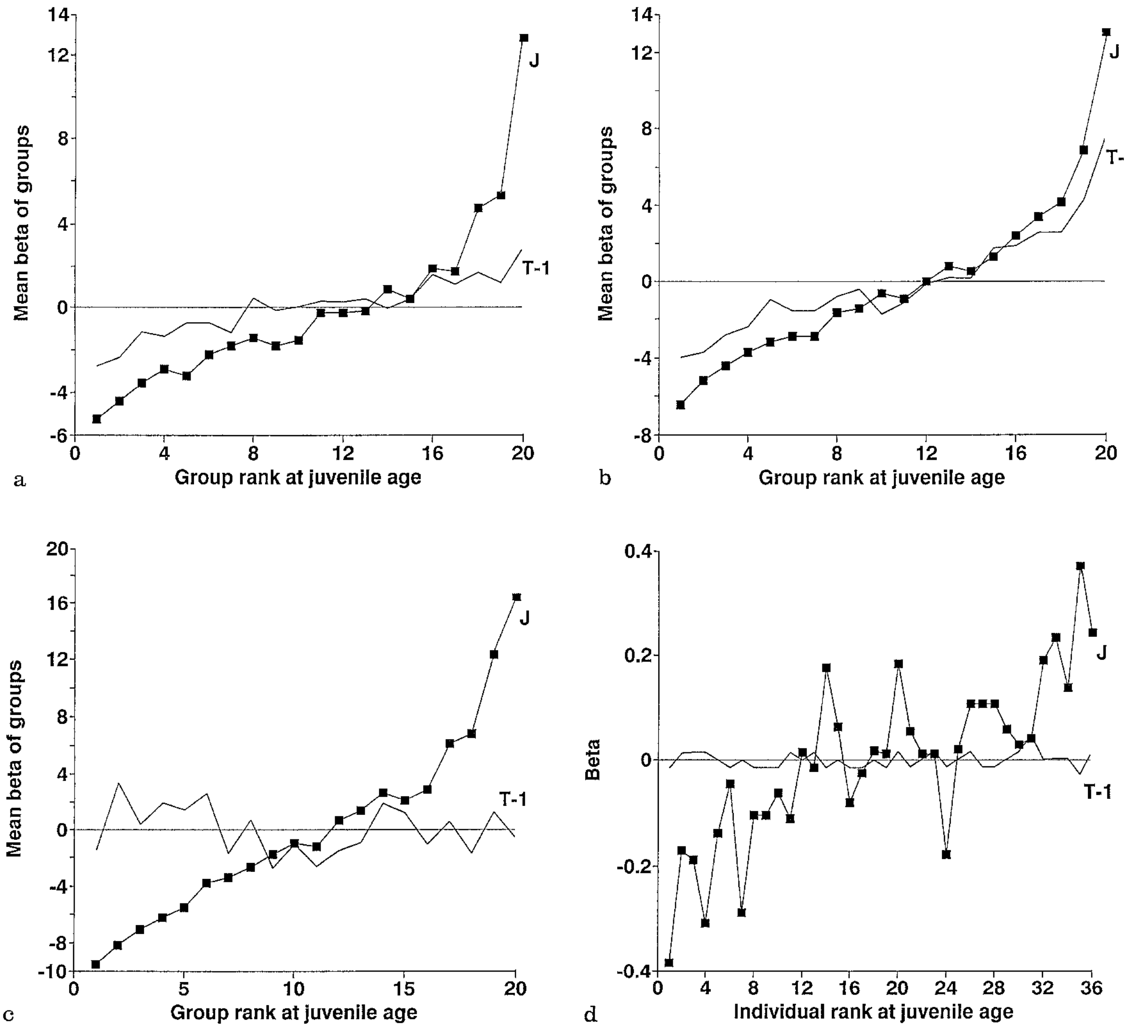

Fig. 3a–d. Ranked group mean (or individual) deviations ($\bar{\beta}$ or β) from the overall mean of relative growth rate (α). *J* Youngest juvenile age, *T*−*1* one age class before the mature age.
In the second group, the actual values are multiplied by some constants (k) to magnify the actual values. k = 60 for both jack pine populations, k = 200 for Norway spruce, and k = 1 for red pine

frequently in forest tree species. Consequently, observed juvenile-mature correlation coefficients, in general, are likely to overestimate the degree of association among extreme individuals.

e. Primary cause for increase in $r_{SS'}$

We have seen that both $\alpha\sqrt{V(S)}$ and the absolute value of $C(\beta)$ decrease. The decrease in absolute values of $C(\beta)$ means increase in $C(\beta)$. Therefore, we may say that $\sqrt{V(S)}$ and $C(\beta)$ are the two components of (5) which increase with age. However, it is more proper to determine which of the two components of (3), $\sqrt{V(S)}$ and $C(S, D)$, increase with age. In all populations except RC, the $Cov(S, D)$ decreased with age. In these populations, $\sqrt{V(S)}$ was the main component which helped increase the $r_{SS'}$. In RC, $Cov(S, D)$ increased as well as $\sqrt{V(S)}$, and their contibutions toward the increase in $r_{SS'}$ were about the same (Table 2). It was predicted in Section IId that $C(S, D)$ will tend to decrease when it is positive initially, while the opposite will hold when it is negative initially. Therefore, the increase in $C(S, D)$ in RC follows the prediction. In RS9, $C(S, D)$ decreased and does not follow the prediction. In RS11, the pattern in unclear (Table 2).

A key question associated with $r_{SS'}$ is: under what conditions will $C(S, D)$ initially be negative and increase with age? Alternately, is the negative $C(S, D)$ unique to red pine or could it occur in other species? The available data sets do not offer a clear answer to these questions because stage of growth and species are confounded – i.e., jack pine and Norway spruce are younger and have positive $C(S, D)$, while red pine populations are older and have negative C(S, D). If we assume that negative C(S, D) can occur in other species as well, then the most likely condition which would lead to negative C(S, D) is a high $\sqrt{V(S)}$ at an earlier juvenile stage. This conclusion is drawn from the mathematical fact that C(S, D) is negative when $\sqrt{V(S)} > r_{SS'}$ (from Eq. (3)). Therefore, when $V(S) > V(S')$, as shown in RS11, C(S, D) is necessarily negative. Since the variance of size in forest trees will not increase indefinitely, it is conceivable that we could get negative C(S, D) in most tree species depending on how we choose juvenile stage and mature stage.

f. Juvenile selection and C (S, D)

Contrary to $r_{SS'}$, which increases with age, C(S, D) is likely to decrease with age when it is positive initially. This implies that there exists a juvenile age when C(S, D) is maximum. Figure 4 shows that such maximum ages tend to exist at earlier juvenile ages in jack pine and Norway spruce populations. It also shows that although all C(S, D) eventually decrease, different populations have different levels of C(S, D).

Since C(S, D) is the component of $r_{SS'}$ which reflects the degree of association between juvenile size and subsequent growth, it is reasonable to expect that C(S, D) would influence the probability of selecting, at an early age, individuals that would be selected at the mature age. In jack pine and Norway spruce, the top 20 individuals were selected at all the ages to see how many of them were included in the mature selection group (Table 3). Although C(S, D) was higher in younger ages (Fig. 4), smaller numbers of early selected individuals were included at mature ages (Table 3). This tendency is not surprising. Even if C(S, D) is smaller for older juvenile individuals, the actual sizes are greater and $\sqrt{V(S)}$ tends to be greater. For example, if we define mature age as the oldest juvenile age, then $C(S, D) = 0$, $\sqrt{V(S)} = r_{SS'} = 1$, and all 20 are included in the final selection. This implies that within a given population, C(S, D) (or r_{SD} defined in Section II a) cannot replace $r_{SS'}$ as a parameter useful for determining gain from juvenile selection.

By examining different populations at comparable stages – i.e., when $\sqrt{V(S)}$ is similar – we can see that different levels of C(S, D) definitely influence the number of individuals selected in these populations (Table 3). Thus, when we have populations with similar growth rates and $\sqrt{V(S)}$ it is possible to use C(S, D) as an indicator of which population might benefit most from early selection.

All the red pine populations have negative C(S, D). It is also possible that c(s, d) are negative in these populations. When $c(s, d) < 0$, $\Delta G_{T|t} < \Delta G_T$ (Eq. (18)), and the actual amount of genetic gain obtainable at the mature stage is less than at the juvenile stage. In this case it would be better not to be concerned about performance at ma-

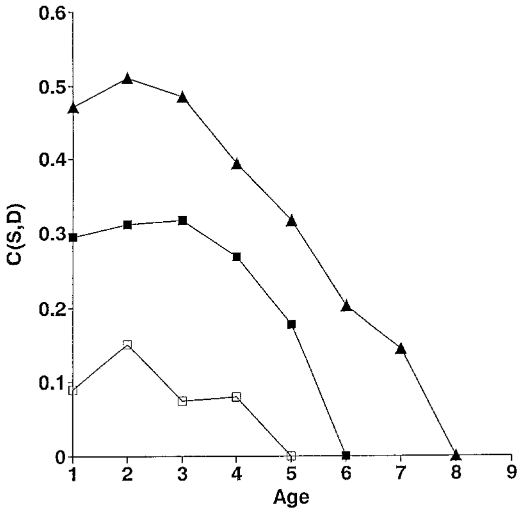

Fig. 4. C (S, D) values of jack pine and Norway spruce populations. *JP* Jack pine parent population, *JO* jack pine offspring population, *NS* Norway spruce

Table 3. Number of 20 juvenile-selected individuals included at the mature selection

Jack pine parent

Mature age	Juvenile age 1	2	3	4	5
6	0	2	6	6	8
5	2	5	7	7	
4	0	5	12		
3	0	5			
2	2				

Jack pine offspring

Mature age	Juvenile age 1	2	3	4
5	0	0	1	6
4	1	2	4	
3	0	5		
2	4			

Norway spruce

Mature age	Juvenile age 2	3	4	5	6	7	8
9	4	5	4	8	9	12	13
8	7	7	7	10	11	15	
7	6	9	7	12	13		
6	5	6	8	14			
5	6	10	11				
4	5	9					
3	6						

ture stages at all. A similar conclusion might be drawn in populations with positive but small c(s, d). For example, jack pine offspring population has small C(S, D). If we assume that $c(s, d) \approx C(S, D)$, we would conclude that the additional gain from $[c(s, d)/\sigma_s]\ \Delta G_T$ is not large enough to consider making juvenile selection for the mature size.

VI. Concluding remarks

The primary applied contribution of this study is that breeders can examine the components of juvenile-mature correlations, and make breeding decisions that would not have been possible based on the correlation coefficients alone. Even if the overall genetic gain might be the same for populations with the same genetic correlation coefficient, the selection strategy may still vary depending on the nature of the components. The forest tree examples indicate that different populations tend to have different levels of C(S, D) (or c(s, d)) at comparable growth stages. In populations with negative or small c(s, d), breeders may do better by making direct juvenile selections. Indirect juvenile selection is desirable when c(s, d) is positive and large. For example, by examining $r_{SS'}$, $\sqrt{V(S)}$, and C(S, D) in Table 2 and assuming that these represent genetic parameters, it can be concluded that: (1) indirect juvenile selection may be avoided in red pine populations; (2) indirect juvenile selection is likely to make little impact in jack pine offspring population; and (3) indirect juvenile selection will be effective in the Norway spruce (and possibly in the jack pine parent) population.

Generally, the increase in juvenile-mature correlation with age is due to the increase in the variance of size (Namkoong and Kang 1990). Consequently, the increasing indirect gain from juvenile selection primarily comes from the proportion of the gain corresponding to the increased direct juvenile selection. To better understand the inheritance of juvenile-mature correlation we need to understand how the pattern of increase in variance is inherited.

It is also clear that increases in the mean relative growth and the variance of size strongly influence the $\mathrm{Cov}(S, \beta S)$, which is the sole covariance term in C(S, D). If the variance of mature size $V(S') < (1+\alpha)^2\, V(S)$, then the sign of $\mathrm{Cov}(S, \beta S)$ will be always negative. A simple applied rule of thumb that can be gleaned from this relation is that indirect juvenile selection is likely to be more useful in slower growing forest tree populations.

It is critical to define the proper mature ages as well as the juvenile selection ages. In general, a useful strategy is to find the mature age when the genetic variance is maximum, then look for the presence of juvenile age at which $\alpha/\sqrt{V(S)}$ is minimum. To develop such strategies, it is essential to study the growth curves of the mean and variance of size.

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Apppendix A. Extension of Equations (5) and (6) to the situation where the family structure of the population is known

If we know the family structure of the population we may rewrite (1)

$$S'_{jk} = S_{jk} + D_{jk} = S_{jk} + (\alpha + \theta_j + \varepsilon_{jk})\, S_{jk}, \tag{22}$$

where

j, k index families and individuals within family, respectively,

$\delta_{jk} = D_{jk}/S_{jk}$,

$\alpha = \left(\sum_{j=1}^{L} \sum_{k=1}^{m(j)} \delta_{jk}\right)/N$,

$\gamma_{jk} = \delta_{jk} - \alpha$,

$\theta_j = \left(\sum_{k=1}^{m(j)} \gamma_{jk}\right)/m_j$,

$\varepsilon_{jk} = \gamma_{jk} - \theta_j$,

$N = \sum_{j=1}^{I} m_j$, and

L = the number of families.

$m_j = {}^{m(j)} =$ number of individuals in j^th family.

Then,

$$\begin{aligned} \mathrm{Cov}(S, S') &= V(S) + \mathrm{Cov}[S, (\alpha + \theta + \varepsilon)\, S] \\ &= V(S) + \alpha V(S) + \mathrm{Cov}(S, \theta S) + \mathrm{Cov}(S, \varepsilon S), \text{ and} \end{aligned}$$

$$r_{SS'} = \sqrt{V(S)} + \alpha\sqrt{V(S)} + \mathrm{Cov}(S, \theta S)/\sqrt{V(S)} + \mathrm{Cov}(S, \varepsilon S)/\sqrt{V(S)} \tag{23}$$

$$r_{SS'} = (1+\alpha)\sqrt{V(S)} + \mathrm{Cov}(S, \theta S)/\sqrt{V(S)} + \mathrm{Cov}(S, \theta S)/\sqrt{V(S)}. \tag{24}$$

The α represents the overall mean of relative growth rates. The θ represents the family mean of the deviation in the growth rate of the individuals from α, and ε represents the deviation in the growth rate of the individuals from θ_j. The β in (5) is the sum of θ and ε. Equations (6) and (24) are equivalent, and $\mathrm{Cov}(S, \beta S)/\sqrt{V(S)} = \mathrm{Cov}(S, \theta S)/\sqrt{V(S)} + \mathrm{Cov}(S, \theta S)/\sqrt{V(S)}$. Therefore, the subdivision of $C(\beta)$ results in subcomponents which are both functions of variance and covariance (Section II b).

Appendix B. Data

Data for two jack pine populations (JP and JO) are the same as those published in Rudolph et al. (1989), where JP and JO represent jack pine parent and jack pine offspring, respectively. From JP, female parents for JO were selected. Seedlings of JP were planted in the Hugo Sauer nursery at Rhinelander, Wisconsin in 1976, and transplanted to the Harshaw Forest Research Farm near Rhinelander in 1978. Tree heights were measured six times between ages 1 through 6, and 1,342 individuals had six measurements. Seedlings of JO were planted in the Hugo Sauer nursery in 1981, and were left in the nursery until the completion of five height measurements, ages 1 through 5. The total number of individuals with complete records was 1,683.

Data for red pine were obtained from the North Central Forest Experiment Station at Grand Rapids, Minnesota. A red pine population at Chippewa National Forest, Minnesota (RC) was established in 1937 as a seed source study, which was later converted into a growth and yield study. Tree height was measured eight times between ages 14 and 46. Complete records were available for 36 individuals. In 1958 a red pine plantation was established at Spooner, Wisconsin to study the effects of spacing and thinning. From this study, two populations with different spacings were derived. The spacing of the first population (RS9) was 9′ × 9′, and that for the second population (RS11) was 11′ × 11′. Heights were measured four times between ages 6 and 26, and a total of 35 and 80 complete data were available for the first and second populations, respectively.

Data for the Norway spruce population (NS) were obtained from a nursery study on height and phenologic characters in Uppsala, Sweden (Eriksson and Ekberg, in preparation). The seeds were sown in 1978, and the seedlings were planted in the nursery in 1979. Eight height measurements between ages 2 and 9 were made, and 798 individuals with complete records were available.

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