Theor Appl Genet (1991) 82:305–312

Index selection with nonlinear profit function as a tool to achieve simultaneous genetic gain

S. Magnussen

Forestry Canada, Petawawa National Forestry Institute, PO Box 2000, Chalk River, K0J 1J0 Ontario, Canada

Received January 3, 1991; Accepted February 20, 1991
Communicated by P.M.A. Tigerstedt

Summary. Simultaneous improvement of several, and often negatively correlated, traits is frequently a desired objective in forest tree breeding. A profit function that includes a combination of both linear weights and weights for the cross-products of trait combinations facilitates the construction of a linear index, with an attractive response in all traits. A detailed algorithm for finding the index coefficients is provided, along with three examples of applications in tree breeding. The index is also a powerful tool in optimizing the selection for a ratio of two traits. It is argued that a more equal progress in several traits provides a safetey net when faced with economic uncertainties. The provided algorithm eliminates the need for direct search techniques. Existence of a dual set of linear weights means that the statistical properties of the index based on nonlinear profit functions are identical to those of the classical Smith-Hazel type of index.

Key words: Selection index – Nonlinearity – Ratios – Genetic gain – Multitrait trade-offs

Introduction

Index selection presents tree breeders with the attractive option of combining information from several traits/sites into a single index with a maximum correlation to the additive genetic merit of the traits (Cotterill 1985; Cotterill and Jackson 1985). Genetic progress using the Smith-Hazel type of selection index (Smith 1936; Hazel 1943) is widely expected to be better than most alternative indices (Hazel and Lush 1942; Harris 1964; Turner and Young 1969). Flexibility with respect to constraints on the expected genetic response increases the utility of index selection in breeding (Kempthorne and Nordskog 1959; Cunningham et al. 1970; Harville 1975; Tai 1977; Itoh and Yamada 1988 a).

A perceived shortcoming of the traditional Smith-Hazel index is its limitation to a linear profit function (Baker 1986). In a linear profit function, the overall value of improvement is determined as the sum of the separate values arising from improvements in each individual trait. There is no allowance for an economic interaction between the traits. In forestry, the crop value attained by improving one trait quite often depends on the level of improvement in other traits. For example, the value of improving stem straightness will increase in proportion to the expected volume gain. A similar rationale holds for improvement in most quality-related traits. In short, what the breeder sometimes wants is to improve combinations of traits simultaneously, instead of gaining a lot in a single trait at the "expense" of others. A long rotation crop, such as trees, with many traits at a favorable level may, indeed, be more valuable in a market with shifting economic preferences than one with only one or a few traits at superior levels.

This study shows how a linear index based on a profit function that includes cross products of the traits can facilitate simultaneous improvement of traits or trait ratios, regardless of their correlation structure. The derivation of index weights for the nonlinear profit function has been generalized by Itoh and Yamada (1988 b). Algorithms for approximate solutions for the quadratic and cubic merit functions have been known for some time (Wilton et al. 1968; Rønningen 1971). The index solution advocated by Itoh and Yamada (1988 b) is intuitively appealing. First, the multivariate normal response surface of genetic gain for a certain selection ratio is defined in terms of sample estimates of the phenotypic and genetic variances and covariances. Next, the economic value of the feasible genetic responses is calculated via the profit function and, third, the optimum profit is determined by classical optimization procedures. Coefficients for the resulting linear selection index are obtained in retrospect once the optimum response has been determined.

Although the problem of assigning weights to traits is notorious in tree breeding (Bridgwater et al. 1983; Zobel and Talbert 1984; Magnussen and Keith 1990), one way to ameliorate the problem is to explore the effects of a range of weights on the selection response and then to choose the "best" set of weights (King et al. 1988). For two or three traits this procedure may be manageable, but it quickly becomes unwidely when more traits are considered. A simple expansion of the proposed index based on a nonlinear profit function offers a simplified and easier method to explore the significance of interactive economic weights.

The index

Consider the task of finding a linear index I for m traits, with a phenotypic variance-covariance matrix **P** and an additive genetic variance-covariance matrix of **G**. Sample estimates are used for both **P** and **G** without further distinction (Harris 1964). From classical index theory based on the properties of multivariate normal distributions (see, e.g., Falconer 1981), we expect the feasible response vector $\boldsymbol{d}$ (dimension m) arising from selection with an intensity of $\mathbf{i}$, to be constrained within the following response surface g (the * symbol is used for transposed matrices; arrows are used to indicate vectors, and bars to indicate a matrix):

$$g(\boldsymbol{d})=\vec{\boldsymbol{d}}^{*}\times\bar{\mathbf{G}}^{-1}\times\bar{\mathbf{P}}\times\bar{\mathbf{G}}^{-1}\times\vec{\boldsymbol{d}}-\mathbf{i}^{2}=0. \tag{1}$$

For a given profit function $f(\boldsymbol{d})$, the task is now to optimize the economic merit of this response ($\boldsymbol{d}$). The profit function chosen here is limited to the form:

$$f(\boldsymbol{d})=\vec{\boldsymbol{a}}^{*}\times\vec{\boldsymbol{d}}+k\times\vec{\boldsymbol{d}}^{*}\times\bar{\mathbf{A}}\times\vec{\boldsymbol{d}}, \tag{2}$$

where $\boldsymbol{a}$ is a vector of linear economic weights (a_i, $i=1,\ldots,m$), and **A** is a $m\times m$ matrix of economic weights (a_{ij}; $i,j=1,\ldots,m$) assigned to the cross products and quadratic terms of the traits in $\boldsymbol{d}$. The factor k is a scaling constant that indicates the weight given on nonlinear trait combinations, as opposed to the weights ($\boldsymbol{a}$) given the individual trait responses. Only symmetric **A** matrices with zero along the diagonal shall be considered, i.e., there are no squared traits in the nonlinear part of the profit function. The symmetry is given by the commutative law of multiplication. Thus, all nonlinear contributions to the profit function arise from two-trait cross products. When k is zero, the nonlinear profit function is identical to the traditional linear merit function. For an index of m traits, the profit function reads (for $k=1$):

$$f(\boldsymbol{d})=\sum_{i=1}^{m}a_i\times d_i+\sum_{i\neq j}^{m}\sum_{j\neq i}^{m}a_{ij}\times d_i\times d_j. \tag{3}$$

Maximization of Eq. 2 under the constraint of Eq. 1 is accomplished by first forming the Lagrange function $F(\boldsymbol{d},\lambda)=f(\boldsymbol{d})+\lambda\cdot g(\boldsymbol{d})$, ($\lambda$ is the Lagrange multiplier) and then finding a feasible saddle point of this function (Gellert et al. 1975). Specifically, we are looking for a solution to the following pair of differential (∂) equations:

$$\left(\frac{\partial F}{\partial d},\frac{\partial F}{\partial \lambda}\right)=(0,0). \tag{4}$$

Both $f(\boldsymbol{d})$ and $g(\boldsymbol{d})$ are quadratic forms with simple derivatives ($\partial^{*}\vec{\boldsymbol{d}}/\partial\vec{\boldsymbol{d}}=\vec{\boldsymbol{d}}$, and $\partial\vec{\boldsymbol{d}}^{*}\bar{\mathbf{A}}\vec{\boldsymbol{d}}/\partial\vec{\boldsymbol{d}}=2\bar{\mathbf{A}}\vec{\boldsymbol{d}}$; Searle 1982). The Newton-Raphson iteration method (e.g., Weir 1990) was used to find the solution $\Phi=\{\boldsymbol{d},\lambda\}$ to Eq. 4. The iterations proceeded in the following fashion:

$$\phi_{\text{new}}=\phi_{\text{old}}+I^{-1}(\phi_{\text{old}})\times S(\phi_{\text{old}}) \tag{5}$$

where $I(\phi_{\text{old}})=\left[\frac{\partial\partial F(\phi)}{\partial\phi^{2}}\right]_{\phi=\phi_{\text{old}}}$

and $S(\phi_{\text{old}})=\left[\frac{\partial F(\phi)}{\partial\phi}\right]_{\phi=\phi_{\text{old}}}$.

An initial value of Φ_{old} was obtained from the index solution $\mathbf{b}_0$ presented by Wilton et al. (1968):

$$\vec{\mathbf{b}}_0=\bar{\mathbf{P}}^{-1}\times\bar{\mathbf{G}}\times(2\times\bar{\mathbf{A}}\times\vec{\boldsymbol{\mu}}+\vec{\boldsymbol{a}}) \tag{6}$$

which yields $\vec{\boldsymbol{d}}_0=\dfrac{\mathbf{i}\times\bar{\mathbf{G}}\times\vec{\mathbf{b}}_0}{\sqrt{\vec{\boldsymbol{b}}_0\times\bar{\mathbf{P}}\times\vec{\boldsymbol{b}}_0}}$.

$\boldsymbol{\mu}$ is the vector of the m trait means. In this study all traits have been adjusted to a zero mean by subtraction of the observed mean. From the initial $\vec{\boldsymbol{d}}_{\text{old}}$ and the condition in Eq. 4, we obtained the initial λ_{old} as (Itoh and Yamada 1988b):

$$\left[\frac{\partial F}{\partial d}\right]_{d=d_0}=0, \tag{7}$$

which yields

$$\lambda_0=\frac{(\vec{\boldsymbol{d}}_0^{*}\times\bar{\boldsymbol{G}}^{-1}\times\bar{\boldsymbol{P}}\times\bar{\boldsymbol{G}}^{-1})\times(2\times\bar{\boldsymbol{A}}(\vec{\boldsymbol{d}}_0+\vec{\boldsymbol{\mu}})+\vec{\boldsymbol{a}})}{-½\times(\vec{\boldsymbol{d}}_0^{*}\times\bar{\boldsymbol{G}}^{-1}\times\bar{\boldsymbol{G}}^{-1})\times(\bar{\boldsymbol{G}}^{-1}\times\bar{\boldsymbol{P}}\times\bar{\boldsymbol{G}}^{-1}\times\vec{\boldsymbol{d}}_0)}.$$

Iterations were stopped when $\max(\vec{\mathbf{d}}_{\text{new}}-\vec{\mathbf{d}}_{\text{old}})<0.0001$ (with the maximum taken over all traits). Convergence was always reached after four iterations and, in most cases, after only two.

From the final estimates of the response vector $\vec{\boldsymbol{d}}$, which optimizes Eq. 2, the index coefficient $\vec{\mathbf{b}}$ was found by equating (in retrospect) the desired response $\vec{\boldsymbol{d}}$ to the (Lin 1978) response $\bar{\mathbf{G}}\cdot\vec{\mathbf{b}}\cdot i/\sigma_I$ expected from a linear index I, and solving for $\vec{\mathbf{b}}$ (the scaling factor i/σ_I can be dropped).

Application

Example 1: selection for stem diameter and wood density

The example illustrates how a nonlinear profit function can solve the dilemma of simultaneous improvement of negatively correlated traits. From King et al. (1988) we have the following sample estimates of the phenotypic (**P**) and additive genotypic (**G**) variance-covariance matrices in Douglas fir progenies at age 12:

$$\bar{\mathbf{P}}=\begin{array}{|cc|}\text{diam.} & \text{dens.}\\ 134.1 & -134.7\\ -134.7 & 639.7\end{array}$$

$$\bar{\mathbf{G}}=\begin{array}{|cc|}\text{diam.} & \text{dens.}\\ 31.4 & -71.0\\ -71.0 & 572.3\end{array}. \tag{8}$$

The phenotypic and genotypic correlation coefficients between the diameter at breast height (diam.; unit: cm) and relative wood density (dens.; unit: kg/m^3) were -0.46 and -0.53, respectively.

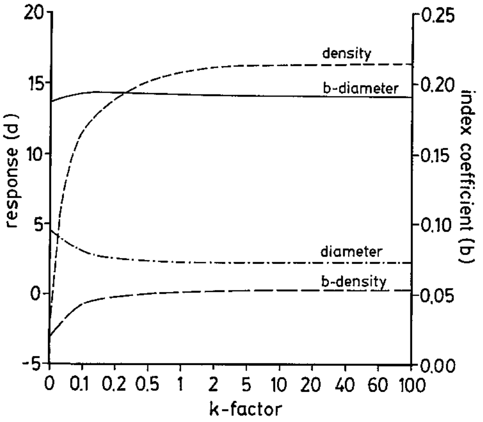

Fig. 1. Response in diameter and density (left y-axis) and index coefficients (right axis) versus k-factor in the nonlinear profit function

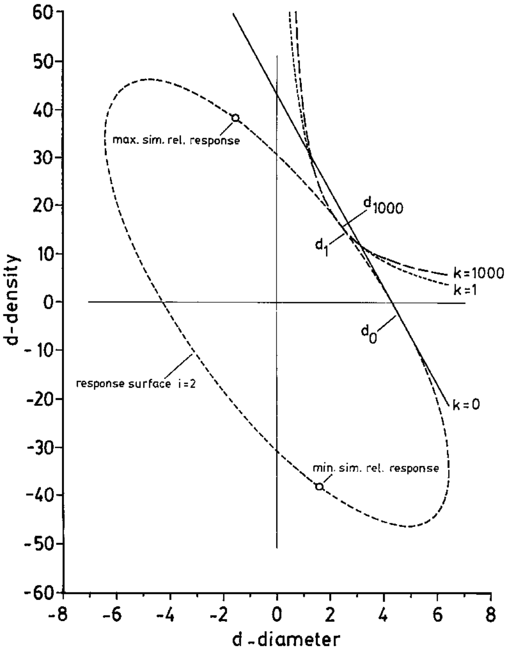

Fig. 2. Optimum response (d) for one linear ($k=0$) and two nonlinear ($k=1$ and $k=1{,}000$) profit functions

For this example assume that the merit function is: $f(\boldsymbol{d}) = 10 \cdot d_{\text{diam.}} + 1 \cdot d_{\text{dens.}} + 2k \cdot d_{\text{diam,}} \cdot d_{\text{dens.}}$ (the factor 2 for the $d_{\text{diam.}} \cdot d_{\text{dens.}}$ term arises from the symmetric properties of $\bar{\mathbf{A}}$). In a linear context ($k=0$), this would indicate that the economic benefit of 1 mm improvement of diameter is ten times as high as the benefit from improving wood density by 1 kg/m^3. For $k>0$ the benefit of improving diameter increases in proportion to the improvement of density and vice versa. The optimum response and index coefficients are depicted in Fig. 1 for a selection ratio of 2.063 (5%) for various values of k. At $k=0$ (i.e., the profit function is linear) the response in diameter was positive (4.5 mm), whereas the density response was negative (-2.1 kg/m^3). The corresponding index coefficients were 0.19 and 0.020. As k increased, the diameter response was slightly reduced, while the index coefficient for diameter remained almost unchanged. The corresponding results for density increased with k. These changes were more pronounced for k values below 0.5 than above, where the response and index coefficients rapidly approached an asymptote. To find the asymptotic values set $\vec{a} = \{0, 0\}$ so that the profit function becomes: $f(\boldsymbol{d}) = d_{\text{diam.}} \cdot d_{\text{dens.}}$. Faced with this reduced profit function, the following optima were computed: $\boldsymbol{d} = \{2.29, 16.46\}$ and $\boldsymbol{b} = \{0.192, 0.0526\}$. In relative terms this response amounted to a 2.6% improvement of diameter and a 4.5% improvement of wood density. King et al. (1988) opted for this solution after a direct search among the response vectors for a wide range of linear economic weights.

A geometrical interpretation of the optimum index solution is provided in Fig. 2. All feasible selection responses for $i=2.063$ are located on the ellipsoid. Three profit functions for $k=0$ (the linear case), $k=1.0$, and $k=1{,}000$ have been drawn. When $k \neq 0$ the profit function becomes a hyperbola. Optimum solutions for the hyperbolic profit functions are found at the vertices, and for the linear model at the contact point of the tangent, with a slope of -10, with the response ellipsoid. Note that the asymptotic solution coincides with the "Maximin" solution found by a direct search among all possible economic weight combinations (King et al. 1988).

If the traits at the onset can be considered equally important, the maximum relative simultaneous response can be determined by an algorithm developed by Magnussen (1990). For this particular example, the two solutions that promise the maximum sum of the relative progress in each trait have been indicated in Fig. 2. They are characterized by a substantial gain in one trait at the expense of progress in the other.

Example 2: selection for volume and wood quality in jack pine

The traits to improve are stem volume, heartwood content, wood density, and stem taper (Magnussen and Keith 1990). From a 20-year-old progeny trial we obtained the phenotypic (**P**) and genotypic (**G**) matrices listed in Eq. 9. We wanted to reduce heartwood content and taper while increasing volume and wood density. With taper defined here as the ratio of stem diameter at half the tree height to the diameter at breast height, a reduction in taper is achieved by increasing the numerical value of this ratio (Ex. 4 shows, in principle, how taper could be improved by selection on the two associated diameters).

$$\mathbf{P}=\left|\begin{array}{cccc} \text{volume} & \text{heartw.} & \text{dens.} & \text{taper} \\ 24524.10 & -22.14 & -95.04 & 265.51 \\ -22.14 & 23.07 & -15.26 & -2.59 \\ -95.04 & -15.26 & 562.00 & 5.20 \\ 265.51 & -2.59 & 5.20 & 52.93 \end{array}\right|$$

$$\mathbf{G}=\left|\begin{array}{cccc} \text{volume} & \text{heartw.} & \text{dens.} & \text{taper} \\ 2224.00 & 27.52 & -96.00 & 166.72 \\ 27.52 & 6.60 & -5.20 & -4.92 \\ -96.00 & -5.20 & 228.00 & 4.52 \\ 166.72 & -4.92 & 4.52 & 17.16 \end{array}\right| . \qquad (9)$$

The profit model chosen to illustrate this example is listed in Eq. 10 (row order: volume, heartwood percent density, and taper).

$$f(\vec{d})=\begin{pmatrix} 100 \\ -1 \\ 10 \\ 1 \end{pmatrix}^{*} \times \vec{d}+k\times\vec{d}^{*}\times\begin{pmatrix} 0 & -5 & 20 & 5 \\ -5 & 0 & 1 & 1 \\ 20 & 1 & 0 & 1 \\ 5 & 1 & 1 & 0 \end{pmatrix}\times\vec{d}. \qquad (10)$$

Volume is clearly given the highest linear economic weight, in agreement with an earlier study (Magnussen and Keith 1990) which indicated that emphasis on volume would generate acceptable progress in the remaining traits. The cross product weights in A express a desire to reward and/or penalize simultaneous responses in pairs of traits. For example, an improvement of volume by one unit is valued at 20 extra points for every concomitant unit of improved wood density. In a similar fashion, a unit improvement of volume is penalized by 5 points if the heartwood is also increased by 1 unit.

Changes in the optimum response vector for various k-values are shown in Fig. 3; the corresponding changes in the index coefficients are presented in Fig. 4. An increase in k from 0 to 0.20 invoked substantial changes in the volume and density response, whereas the response of heartwood and taper only underwent minor changes. The effect of the cross product matrix $\bar{\mathbf{A}}$ on the selection outcome was the desired one. Rewarding simultaneous improvement of volume and wood density resulted in a reversal of the response in density from -1 to $+6$ kg/m^3, accompanied by a drop in the response of volume from 26 to 18 dm$^3 \cdot 10^{-1}$. Changes in heartwood response, although minor, were attractive. Only the slight reduced response in taper was counter to the desired changes. The asymptotic responses were those obtainable with the profit function $f(\vec{d})=\vec{d}^{*}\cdot\bar{\mathbf{A}}\cdot\vec{d}$; they differ less than 0.1% from the results shown for $k=20$ in Fig. 3.

Changes in index coefficients obviously alter the set of trees selected. Figure 5 shows the relationship between the index for $k=1$ (nonlinear profit function, almost asymptotic) and the index based on a linear profit function ($k=0$) when the top 5% of the trees was selected. Although the overall relationship was tight ($r=0.91$), one-third of the trees selected by one of the indices would not have been selected by the other. Similar results were

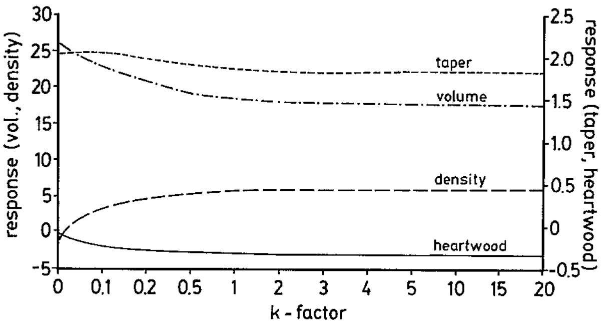

Fig. 3. Optimum response in volume, heartwood, density, and taper for various k-factors in the profit function (Eq. 10)

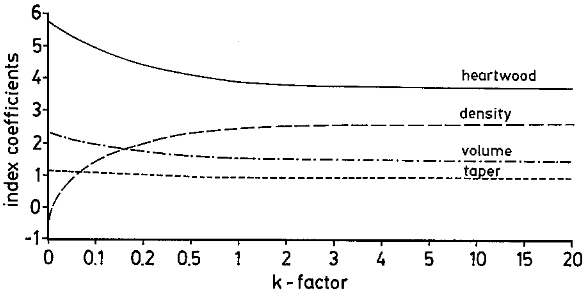

Fig. 4. Optimum index coefficients for volume, heartwood, density, and taper for various k-values in the profit function (Eq. 10)

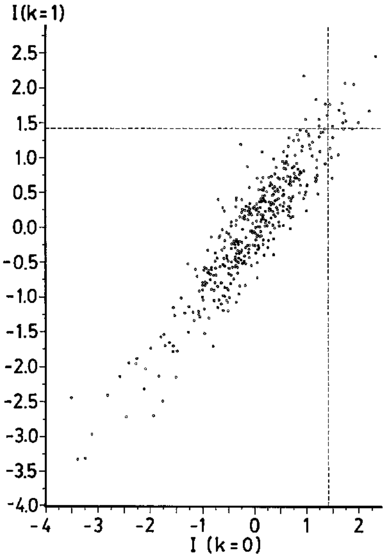

Fig. 5. Selection index I_1 for the quadratic profit function ($k=1$ in Eq. 10) plotted against the selection index I_0 for the linear profit function ($k=0$ in Eq. 10). Traits: volume, density, heartwood, and taper. Dashed lines indicate the 5% selection thresholds for the two indices

obtained at lower selection ratios (10 and 20%). Trees selected exclusively by the index with the linear profit function ($k=0$) had a phenotypic volume and density response of 52.0 dm^3 and -1.8 $\mathrm{kg/m}^3$, respectively. The parallel responses in the trees selected exclusively by the index with $k=1$ were 36.8 dm^3 and 11.5 $\mathrm{kg/m}^3$, a clear indication of the shift towards simultaneous improvement of volume and density.

Example 3: selection for annual height growth in jack pine

The following **P** and **G** variance-covariance matrices were obtained for 4 years annual height growth (h1-h0, h2-h1, h3-h2, and h4-h3) from a jack pine half-sib progeny trial (Magnussen and Yeatman 1987):

$$\bar{\mathbf{P}}=\left|\begin{array}{rrrr} \text{h1-h0} & \text{h2-h1} & \text{h3-h2} & \text{h4-h3} \\ 34.9 & -10.2 & -26.4 & 26.0 \\ -10.2 & 108.1 & 10.6 & -12.0 \\ -26.4 & 10.6 & 487.5 & -72.6 \\ 26.2 & -12.0 & -72.6 & 299.3 \end{array}\right|$$

$$\bar{\mathbf{G}}=\left|\begin{array}{rrrr} \text{h1-h0} & \text{h2-h1} & \text{h3-h2} & \text{h4-h3} \\ 9.6 & -1.7 & -9.5 & 9.3 \\ -1.7 & 40.1 & 25.9 & 3.8 \\ -9.5 & 25.9 & 58.5 & -27.1 \\ 9.3 & 3.8 & -27.1 & 30.8 \end{array}\right|. \qquad (11)$$

Selection is for improved annual height growth within each of the 4 years. The value of a unit improvement in annual height growth is, theoretically at least, independent of the age of the tree[1], but its overall value will depend on both the direct response to selection and the indirect responses due to the correlation with height growth in other years. For these reasons the following profit function was chosen:

$$f(\boldsymbol{d})=\begin{pmatrix} 1 \\ 1 \\ 1 \\ 1 \end{pmatrix}\times\vec{d}+k\times\vec{d}^{*}\times\begin{pmatrix} 0 & 1 & 1 & 1 \\ 1 & 0 & 1 & 1 \\ 1 & 1 & 0 & 1 \\ 1 & 1 & 1 & 0 \end{pmatrix}\times\vec{d}. \qquad (12)$$

Optimum responses for various k-values are graphed in Fig. 6, while the corresponding index coefficient solutions are found in Fig. 7. With k equal to zero, the total expected height growth response by selecting the top 5% of the trees amounted to 15.4 cm or 8.1% of the mean height of all progenies at age 4. Improvement of 2nd and 3rd year's height accounted for 53 and 32%, respectively, of the total improvement. When the value of an improvement in 1 year's growth is proportional to the improvement in the other years ($k>0$), we see a shift in the response towards less improvement in the 2nd and 3rd year and a reverse trend in the improvement of 1st and 4th year's growth. A stable response pattern was reached for $k>0.2$. Overall the total response dropped by 1.4% when k increased from 0 to 20. What the nonlinear profit function achieved was to dampen the ratio of the best (2nd year's growth) to the poorest (1st year's growth) response from 11 to 6. This was also reflected in differences in the rank stability of growth between the trees selected with the linear profit function ($k=0$) and those selected by the nonlinear function ($k=1$). The former group had an average rank correlation (Spearman) of 0.68, while the correlation in the latter group was 0.76. A total of 78% of the trees selected with the linear profit function would also have been selected with the index based on the nonlinear index in Eq. 12. It should be noted that it is possible to obtain an 8.7% gain in height at age 4 with an index based on height and not annual growth (Magnussen 1990). The maximum simultaneous response (Magnussen 1990), which can be considered the biological approach (no a priori weighting), promised 6.2% gain in final

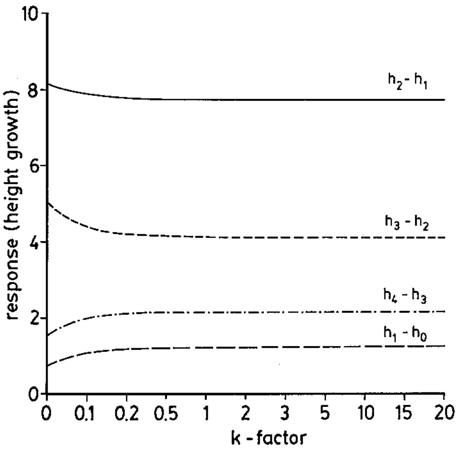

Fig. 6. Response in 4 years annual height growth at various levels of the k-factor in the profit function (Eq. 12)

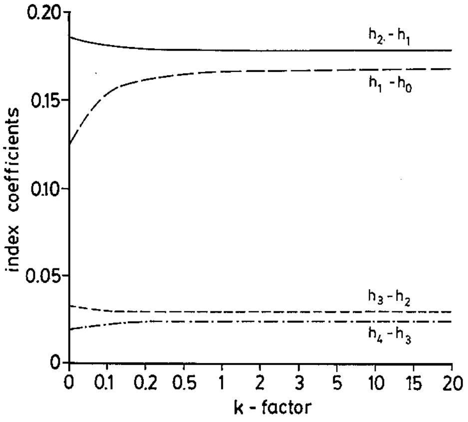

Fig. 7. Index coefficients (weights) for 4 years annual height growth at various level of the k-factor in the profit function (Eq. 12)

---

[1] Rapid early growth may have some major payoffs by requiring less tending

height at age 4. A lower response to selection on periodic growth than selection for final size was also demonstrated by Namkoong and Matzinger (1975) when they selected for weekly growth in *Nicotiana tabacum* L.

Example 4: improvement of traits expressed as ratios

Improvement of the ratio of two traits is often desired in order to increase some measure of production efficiency. The classical examples from dairy improvement are percent milk fat and weight gain to feed consumption. If the two traits in the ratio are both normally distributed, their ratio is not (Turner and Young 1969), and the classical Smith-Hazel type of selection index is no longer applicable. An index with the type of nonlinear profit function used in the previous examples can also be used to find the optimum solutions for selection for a ratio. Existing methods for finding an index for a trait ratio are based on either a linear approximation or a simple selection based on the ratios of univariate breeding values (see Famula 1990 for further details).

From an example, presented by Famula (1990) in a recent note on the problem of optimizing the ratio of two traits x_1 and x_2, we have the following results:

$$\mathrm{E}(x_1, x_2) = (190, 790)$$

$$\bar{\mathbf{P}} = \left|\begin{array}{cc} x_1 & x_2 \\ 235 & 598 \\ 598 & 3708 \end{array}\right|$$

$$\bar{\mathbf{G}} = \left|\begin{array}{cc} x_1 & x_2 \\ 106 & \\ 337 & 1854 \end{array}\right| \quad 337\ . \tag{13}$$

To optimize the ratio x_1/x_2, it is convenient to use the transformation $x_3 = 1/x_2$ and then to recalculate the phenotypic and genotypic variance-covariance matrices by application of the 'Delta technique' (Bulmer 1985, Eq. 6.27, p. 83). After this manipulation the following matrices were obtained:

$$\mathrm{E}(x_1, x_3) = (190, 0.001267)$$

$$\bar{\mathbf{P}} = \left|\begin{array}{cc} x_1 & x_3 \\ 235 & -0.00096 \\ -0.00096 & 9.5 \times 10^{-9} \end{array}\right|$$

$$\bar{\mathbf{G}} = \left|\begin{array}{cc} x_1 & x_3 \\ 106 & -0.00054 \\ -0.00054 & 4.8 \times 10^{-9} \end{array}\right| . \tag{14}$$

The profit function for optimizing x_1/x_2 is hereafter: $F(\boldsymbol{d}) = \vec{\boldsymbol{d}}^* \times \bar{\mathbf{A}} \times \vec{\boldsymbol{d}}$ where $\vec{\boldsymbol{d}} = \{x_1,\ x_3\}$ and $\bar{\mathbf{A}} = \{0\ 0.5,\ 0.5\ 0\}$. Index coefficients (**b**) obtained with this procedures were 0.0786 for x_1 and 11790.7 for $1/x_2$. This index was strongly correlated ($r > 0.990$) with the two alternative indices presented by Famula (1990). Selection based on the above index is expected to increase the ratio (x_1/x_2) from 0.241 before selection to 0.246 for a selection intensity of 1.0. The two indices used by Famula promise the same improvement per unit selection intensity. Application of the principle of maximum simultaneous progress (in x_1 and $1/x_2$) would procedure a shift in the ratio from 0.241 to 0.245 for a unit selection intensity.

Discussion and conclusions

The idea of extending the selection index theory to include nonlinear profit function has been around for some time (Kempthorne and Nordskog 1959; Wilton et al. 1968), but a mathematically correct approach to the solution has recently been provided by Bulmer (1985) and Itoh and Yamada (1988 b). The solutions presented in this study are based on Itoh and Yamada's work. Bulmer's solution addresses the optimization of the progeny value of selected parents, which leads to a search for the optimum assortative mating of the parents. Assortative mating is indeed attractive in the presence of nonlinear profit functions (Allaire 1980; Goddard 1983; Burdon 1990), and it should be considered as an option in the breeding following selection based on nonlinear profit functions (Allaire 1980).

Previous methods for finding index weights in the presence of quadratic profit functions have used an expansion of the phenotypic and genotypic variance-covariance matrices based on expected values (Rønningen 1971), a least-squares solution with expectations of squared random variables (breeding values) (Wilton et al. 1968), or added nonlinear transformation of the traits as new traits to be selected for (Kempthorne and Nordskog 1959). These methods have been criticized for various reasons. Goddard (1983) argued the point that some nonlinear indices were exploiting nonadditive variances and thus overestimating the expected response. He also pointed to the fact that maximizing the genetic merit of the parents is not identical to maximizing the genetic merit of the offspring. Segregation and recombination would tend to dampen the effect of nonlinear profit. This was confirmed in a simulation for a single trait by Burdon (1990). Rønningen (1971) found that inclusion of nonlinear transformations as new traits might confound some of the genetic variances with phenotypic contributions.

The index solution advocated by Itoh and Yamada (1988 b) does not suffer from these shortcomings because it is based on the restriction of the response surface, which is derived directly from the classical Smith-Hazel type of index and multivariate normal theory (Smith 1936; Hazel 1943). All points on the feasible response surface are solutions to the traditional index with a linear merit function. In other words, a set of linear economic weights can be found in retrospect once the desired response has been determined. The desired response is simply the one that maximizes the profit function. Itoh and Yamada's (1988 b) solution is more transparent and logical because it is derived from classical mathematical theory of conditional optimizing of convex target functions (Gellert et al. 1975). Its application to selection for traits expressed as ratios and difference series (growth data) adds to the utility of the herein presented index method (Famula 1990). The abundance of normally distributed traits justifies reliance on normal theory.

Because a set of linear economic weights can be found in retrospect for each solution based on a nonlinear profit function, the accuracy of an index is not affected by inclusion of nonlinear terms in the profit function. Methods outlined by Hayes and Hill (1980) and Tai (1989), to assess the stability and accuracy of an index, apply equally to situations with nonlinear profit functions. A sensitivity analysis of the expected response is always recommended to ensure that expectations remain realistic.

Linear selection indices (namely, linear functions of the phenotypes for different traits) based on nonlinear value functions for crop improvement are especially attractive when desirable trait combinations are negatively correlated and when uncertainties surround the economic weights of individual traits. For the simple model illustrated in this study, additional economic weights were only needed for the trait cross products in order to exploit, in a straightforward manner, the potential for simultaneous improvement in several traits or ratios of traits. When more economic emphasis is placed on the simultaneous improvement of traits, the index solution rapidly approaches an asymptote that can be found by simply dropping the linear term for the profit function. The asymptotic solution will, of course, depend on the pattern of economic weights given to the pair-wise trait combinations. In this respect, the presented index tool is more flexible than the algorithm intended for finding the maximum relative simultaneous solution (Magnussen 1990). Both methods, however, are far superior to the more tedious task of finding a set of suitable economic weights for three or more traits that produces acceptable progress in all traits.

Acknowledgements. Many valuable comments and critical remarks were given to a previous version of this manuscript by Drs. J. Hanover, D. Joyce, and R. D. Burdon. Their help is much appreciated.

References

Allaire FR (1990) Mate selection by selection index theory. Theor Appl Genet 57:267–272

Baker RJ (1986) Selection indices in plant breeding. CRC Press, Boca Raton/FL

Bridgwater FE, Talbert JT, Jahromi S (1983) Index selection for increased dry weight in a young loblolly pine population. Silvae Genet 32:157–161

Bulmer MG (1985) The mathematical theory of quantitative genetics. Clarendon Press, Oxford

Burdon RD (1990) Implications of nonlinear economic weights for breeding. Theor Appl Genet 79:65–71

Cotterill PP (1985) On index selection. II. Simple indices which require no genetic parameters or special expertise to construct. Silvae Genet. 34:64–69

Cotterill PP, Jackson N (1985) On index selection. I. Methods of determining economic weight. Silvae Genet 34:56–69

Cunningham EP, Moen RA, Gjedrem T (1970) Restriction of selection indices. Biometrics 26:67–74

Falconer DS (1981) Introduction to quantitative genetics, 2nd edn. Longman, London

Famula TR (1990) The equivalence of two linear methods for the improvement of traits expressed as ratios. Theor Appl Genet 79:853–856

Gellert WH, Kustner H, Hellwich M, Kastner H (1975) The VNR concise encyclopedia of mathematics. Van Nostrand Reinhold, N.Y.

Goddard ME (1983) Selection indices for nonlinear profit functions. Theor Appl Genet 64:339–344

Harris DL (1964) Expected and predicted progress from index selection involving estimates of population parameters. Biometrics 20:46–72

Harville DA (1975) Index selection with proportionality constraints. Biometrics 31:223–225

Hayes JF, Hill WG (1980) A reparameterization of a genetic selection index to locate its sampling properties. Biometrics 36:237–248

Hazel LN (1943) The genetic basis for constructing selection indices. Genetics 28:476–490

Hazel LN, Lush JL (1972) The efficiencies of three methods of selection. J Hered 33:393–399

Itoh Y, Yamada Y (1988 a) Selection indices for desired relative genetic gains with inequality constraints. Theor Appl Genet 75:731–735

Itoh Y, Yamada Y (1988 b) Linear selection indices for nonlinear profit functions. Theor Appl Genet 75:553–560

Kempthorne O, Nordskog AW (1959) Restricted selection indices. Biometrics 15:10–19

King JN, Yeh FC, Heaman JCH, Dancik DP (1988) Selection of wood density and diameter in controlled crosses of coastal Douglas-fir. Silvae Genet 37:152–157

Lin CY (1978) Index selection for genetic improvement of quantitative characters. Theor Appl Genet 37:152–157

Magnussen S (1990) Selection index: economic weights for maximum simultaneous genetic gain. Theor Appl Genet 79:289–293

Magnussen S, Keith CT (1990) Genetic improvement of volume and wood properties of jack pine: selection strategies. For Chron 66:281–286

Magnussen S, Yeatman CW (1987) Four years height growth of 25 yack pine (*Pinus banksiana* Lamb.) families in an accelerated nursery trial. In: Demeritt ME Jr (ed) Proc 30th NE For Tree Improv Conf School of Forest Research, University of Maine, Orono, July 22–24, 1987, pp 47–64

Namkoong G, Matzinger DF (1975) Selection for annual growth curves in *Nicotiana tabacum* L. Genetics 81:377–386

Rønningen K (1971) Selection index for quadratic and cubic models of the aggregate genotypes. Agricultural College of Norway, Institute of Animal Genetics and Nutrition, Report No. 312

Searle S (1982) Matrix algebra useful for statistics. Wiley and Sons, New York, pp 329–330

Smith HF (1936) A discriminant function for plant selection. Ann Eugen 7:240–250

Tai GCC (1977) Index selection with desired gains. Crop Sci 17:182–183

Tai GCC (1989) A proposal to improve the efficiency of index selection by "rounding." Theor Appl Genet 78:798–800

Turner HN, Young SSY (1969) Quantitative genetics in sheep breeding. Cornell University Press, Ithaca/NY

Weir BS (1990) Genetic data analysis. Sinauer, Sunderland/MA

Wilton JW, Evans DA, Vleck LD van (1968) Selection indices for quadratic models of total merit. Biometrics 24:937–949

Zobel B, Talbert J (1984) Applied forest tree improvement. Wiley and Sons, New York