

Implications of non-linear economic weights for breeding

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Summary. Relationships were studied theoretically between phenotypic values of selection candidates ('parents') and economic worth of the 'offspring' that would belong to production populations. The candidates could include individuals, crosses or clones, and the offspring could be produced either sexually or vegetatively. Cases considered included: three systems for generating production populations [clonal propagation, pair(full-sib)-crosses and half-sib crosses]; three economic-worth (profit) functions for individual offspring (linear, intermediate optimum, acceptable versus cull); and independently varying heritabilities for both parents and offspring. The heritabilities were varied in the model against a background of fixed genetic variance. Parental values were considered in terms of phenotypic standard deviations from the population mean, assuming normality. Lower heritabilities and, to a lesser extent, genetic segregation severely damped down the non-linearities of economic worth in relation to measured parental values, such that the linear weightings for traits in a selection index should usually be a good approximation, provided the profit function for individual offspring is monotonic. The economic advantages of corrective mating within a select population may be minimal if both heritabilities are low and the profit functions apply to individual offspring. The economic advantages accruing from genetic uniformity of clones (or crosses between inbreds) in conjunction with non-linear profit functions are strongly dependent on achieving high broad-sense heritabilities, particularly in the offspring (production population).

Key words: Plant breeding – Economic weights – Non-linearity – Clonal systems – Animal breeding

Introduction

A common assumption in plant and animal breeding is that economic-worth (profit) functions are linear; in other

words, that the economic gain from a given phenotypic difference in the value for a metric trait is constant over the full range of variation. This assumption is fully invoked in an unrestricted Smith-Hazel selection index (Baker 1986; Wricke and Weber 1986) containing linear functions of the phenotypic values for the various traits involved.

In practice, there are obvious departures from the linear relationship within the commercial (or 'production') population. In some cases technical specifications impose thresholds of acceptability, e.g. back fat thickness for carcass grades or knot diameters for sawlog grades, which will mean a stepwise function in relation to phenotypic value. In many, less extreme cases there may be curvilinear 'law-of-diminishing-returns' relationships. These situations are implicitly recognised by certain restrictions (Baker 1986) that have been devised for Smith-Hazel selection indices, e.g.: restrictions to keep unchanged the mean values for one or more traits (Kempthorne and Nordskog 1959); restrictions keeping gains in individual traits to specified levels per unit selection intensity (Tallis 1962); or restrictions that extend the Tallis restrictions to proportionality of gains among all the traits under consideration (Pesek and Baker 1969). A less sophisticated recognition of non-linearity is embodied in independent culling levels. Non-linear profit functions are also part of the implicit rationale for 'corrective mating' (Allaire 1980) between parents. However, the efficacy of these various devices for accommodating non-linear profit functions to maximum advantage seems to have received limited study.

Another type of non-linearity is where any departure from crop or flock uniformity is undesirable per se, or where there is a definite optimum within the range of genotypic variation. This is extremely important for many cash crops where requirements for harvesting and processing demand minimal variability. Genetic segregation, such as typically occurs within pair-crosses of out-

breeders can, of itself, introduce unacceptable variability. With obligate sexual propagation a widespread response, by plant breeders in particular, has been to convert the organism to an inbreeder from an outbreeder. Another response is to produce heterotic and uniform production populations from crosses among inbred lines. Where vegetative propagation is feasible, mass cultivation of clones becomes the classic option.

Thus, three main issues that arise from non-linear profit functions are: (i) The extent to which non-linearity in relation to phenotypic value within the production population invalidates a linear function of the metric values of the selections made. While Baker (1986) concluded that "there is no really satisfactory way of addressing the problem of non-linear worth functions", he did not examine how important the problem is in the first place. Itoh and Yamada (1988) have documented alternative non-linear index solutions, and have cited earlier studies where different workers drew varying conclusions as to whether non-linear index weightings are appropriate. They did not, however, attempt any synthesis to guide breeders as to when the complexities of non-linear solutions should be addressed. (ii) The extent to which, and the circumstances in which, various departures from classical selection indices, viz. restrictions, independent culling levels and corrective mating, are likely to be effective. (iii) The extent to which the theoretical advantages of genetic uniformity are realisable, if the uniformity can be achieved.

Heritability, as influenced by uncontrolled environmental ('noise') variation clearly has a major bearing on all these questions. Such variation, if large, can encompass major departures from linearity, and will thereby tend to damp down the expression of non-linearities in the economic value of crops or flocks produced from selections of varying phenotypes. This damping down of non-linearities is studied here to help answer the three questions. Cases considered involve: clonal systems versus use of both full-sib and half-sib families, types of profit function and a range of heritabilities both in the candidate population from which selections are made and in the production population.

The Model

Candidate ('parental') population

Consider a large candidate population, with the following attributes:

\bar{X} = mean (=0)

additive inheritance

normal distribution

panmixis

x = phenotypic value of an individual candidate

σ_g^2 = genotypic variance (fixed at unity)

σ_x^2 = phenotypic variance

$$= k \sigma_g^2 / h_p^2$$

(1)

h_p^2 = heritability of candidate values, which may include measurements on individuals, means in clonal tests, half-sib family means in progeny tests or full-sib family means

$$= k \sigma_g^2 / \sigma_x^2$$

k = coefficient of relationship, e.g. 1 for clones, 0.5 for random full-sib families, 0.25 for random half-sib families

x' = expected phenotypic value (parental value, clonal mean or half-sib progeny mean) of clone/parent X

$$= X/h_p \text{ (for } \sigma_g^2 = 1\text{)} \quad (2)$$

x'' = expected genotypic value of the phenotype X

$$= X h_p \quad (3)$$

X = phenotypic value, in standard deviations.

Production ('offspring') population

For individual offspring (sexually produced progeny or clonal propagules) of a large number of unselected candidates (assuming same expression of genotypic effects as in candidate population and normality and a mean of zero):

h_o^2 = heritability

$$= \sigma_g^2 / \sigma_o^2$$

σ_o^2 = total phenotypic variance.

For a class of candidates of phenotype X :

y = individual phenotypic value

\bar{y} = class mean

$\approx x'$ (see above) for large n

σ_y^2 = variance about \bar{y}

$$= \sigma_y'^2 + \sigma_y''^2$$

$\sigma_y'^2$ = genotypic variance of clones/parents about \bar{y}

$\sigma_y''^2$ = phenotypic variance within a clone/family

n = number of clones, or families, in class.

Now for n clones:

$$\sigma_y'^2 = \sigma_g^2 (1 - h_p^2) (n-1)/n = (1 - h_p^2) (n-1)/n \text{ (for } \sigma_g^2 = 1\text{)} \quad (5)$$

$$\sigma_y''^2 = \sigma_g^2 / h_o^2 - \sigma_g^2 = 1/h_o^2 - 1 \text{ (for } \sigma_g^2 = 1\text{)} \quad (6)$$

$$\sigma_y^2 \approx 1/h_o^2 - h_p^2 \text{ for large } n. \quad (7)$$

For n pair-cross (full-sib) families:

$$\sigma_y'^2 \approx \frac{1}{2} \sigma_g^2 (1 - h_p^2) (n-1)/n = (1 - h_p^2) (n-1)/2n \text{ (for } \sigma_g^2 = 1\text{)} \quad (8)$$

$$\sigma_y''^2 = (\geq \frac{1}{2} \sigma_g^2) + (\sigma_g^2 / h_o^2 - \sigma_g^2) = \geq 1/h_o^2 - \frac{1}{2} \text{ (for } \sigma_g^2 = 1\text{)} \quad (9)$$

($\geq \frac{1}{2} \sigma_g^2$ denotes segregational variance, and reflects possible departures from an additive genetic model, plus the fact that σ_g^2 might be truncated by prior selection with respect to the base-population value)

$$\sigma_y^2 \geq 1/h_o^2 - h_p^2/2 \text{ for large } n. \quad (10)$$

For n half-sib families, with select parents mated with base-population material:

$$\sigma_y'^2 \approx \frac{1}{4} \sigma_g^2 (1 - h_p^2) (n-1)/n \approx (1 - h_p^2) (n-1)/4n \text{ (for } \sigma_g^2 = 1\text{)} \quad (11)$$

$$\sigma_y''^2 = (\geq \frac{3}{4} \sigma_g^2) + (\sigma_g^2 / h_o^2 - \sigma_g^2) = \geq 1/h_o^2 - \frac{1}{4} \text{ (for } \sigma_g^2 = 1\text{)} \quad (12)$$

$$\sigma_y^2 \geq 1/h_o^2 - h_p^2/4 \text{ for large } n. \quad (13)$$

Note: (1) A case $n=1$ is equivalent to the case $h_p=1$. (2) For clones, h_p^2 is necessarily a broad-sense heritability. For pair-crosses (or half-sib crosses), $\sigma_y''^2$ does not conform exactly to the specified function of h_p^2 . It is overestimated if h_p^2 is a broad-sense heritability and underestimated if h_p^2 is a narrow-sense heritability.

ity, the bias depending on the magnitude and make-up of non-additive gene effects. However, non-additive gene effects would contribute in a higher proportion to σ_y^2 than would the additive gene effects.

Profit functions

The following profit functions ($P = P(y)$) were assumed for individuals:

(1) Linear

$$P = cy + q \quad (14)$$

c is assumed to be $1/3$ and q zero for purposes of illustration. As mentioned earlier, this embodies the classic assumption for an unrestricted Smith-Hazel index.

(2) 'Stepwise'

$$\text{for } y < d, P = 0; \text{ for } y \geq d, P = 1. \quad (15)$$

This reflects an acceptability/cull threshold. The value for d was set arbitrarily at 0.

(3) Normal distribution ('Normal')

$$P = \frac{1}{\sqrt{2\pi}\sigma} e^{-(y-d)^2/(2\sigma^2)}. \quad (16)$$

Assuming $d=0$ and $\sigma=1$, this simplifies to

$$P = \frac{1}{\sqrt{2\pi}} e^{-y^2/2}. \quad (17)$$

This entails an intermediate optimum. With $d=0$, any departure from the candidate population mean is adverse, but d could equal any x'' . The assumed value for σ again is arbitrary, but the importance of departures from the optimum is reflected in σ^{-1} .

Among these three classes of profit functions, the numerical values of individual parameters are not intended to be comparable.

Computation of economic worth

The distribution of phenotypic values of a large number of offspring of phenotype X is given by the normal distribution function:

$$f(y) = \frac{1}{\sqrt{2\pi}\sigma_y} e^{-(y-y)^2/(2\sigma_y^2)} \quad (18)$$

and the economic value (\bar{P}) of the offspring is given by:

$$\bar{P} = \int_{y=-\infty}^{y=\infty} P(y) f(y) dy. \quad (19)$$

Solutions for the integration are given in the Appendix.

Appropriate values for x' and σ_x^2 can be substituted in, according to whether the case involves clones, full-sib families or half-sib families, and varying values of h_p^2 and h_o^2 . This was done for various $P(y)$.

The following cases were considered in all combinations:

- clones, pair-crosses, half-sib families;
- various h_p^2 values in range 0.2–1;
- various h_o^2 values in range 0.05–1;
- various X values in range -3.5 – 3.5 .

Separate plottings of \bar{P} versus X were made for clones, full-sibs and half-sibs, and individual graphs were made for the various profit functions covering the range of h_o^2 for a given h_p^2 and the range of h_p^2 for a given h_o^2 .

Results

For the linear profit function, the expression for \bar{P} duly simplifies to a straightforward linear function of X :

$$\bar{P} = cy (\approx ch_p X) \quad (20)$$

namely, the product of c and the expected genotypic value for phenotype X .

For the stepwise profit function, \bar{P} values are graphed in relation to X , for selected combinations of h_p^2 and h_o^2 , and for clones, full-sib families and half-sib families (Fig. 1). This confirms that as heritabilities get lower, the non-linear component in the relationship of \bar{P} on X becomes less and less, which holds with respect to both h_p^2 and h_o^2 . Also, the non-linearity for given h_p^2 and h_o^2 values is less marked for full-sib families than for clones, and even less for half-sibs, although differences between categories in \bar{P} curves are much less marked with the lower heritabilities.

For the 'normal' profit function with high h_p^2 and X values around the mean, clones have higher \bar{P} values than full-sibs which, in turn, have slightly higher values than half-sibs (Fig. 2). For the combination of extreme X values and high h_p^2 , however, the ranking of clones, full-sibs, and half-sibs for \bar{P} is reversed. For low h_p^2 , the impact of h_o^2 is much reduced (Fig. 3) and the differences between the classes are very minor. For the case $X=0$, and $n=1$ and/or $h_p^2 \rightarrow 1$, Fig. 4 shows the \bar{P} values in relation to h_o^2 for the three classes. This underscores how the profit advantages of clones over sexually propagated material depend strongly on h_o^2 being high. The greatest advantage of clones over full-sibs under the model is 22% and over half-sibs it is 32%.

Discussion

Choice of profit functions

The types of non-linear relationships considered were chosen arbitrarily, but they are both plausible situations that may arise for different traits.

The stepwise function [Eq. (15)] relates to the case of cull-versus-acceptability thresholds, which are a common commercial reality. The percentile point for the culling threshold can obviously vary widely, but there seems to be no reason to believe that such variations would alter the conclusion that low heritabilities and genetic segregation both sharply reduce the non-linearities with respect to parental worth. This function can be regarded as a limiting case among monotonic profit functions. Plausible cases among the other monotonic functions would be multi-stepped functions or roughly sigmoidal ones. A sigmoidal function contains a range in which the relationship is essentially linear; below this range tends to represent outright cull material and above the range the

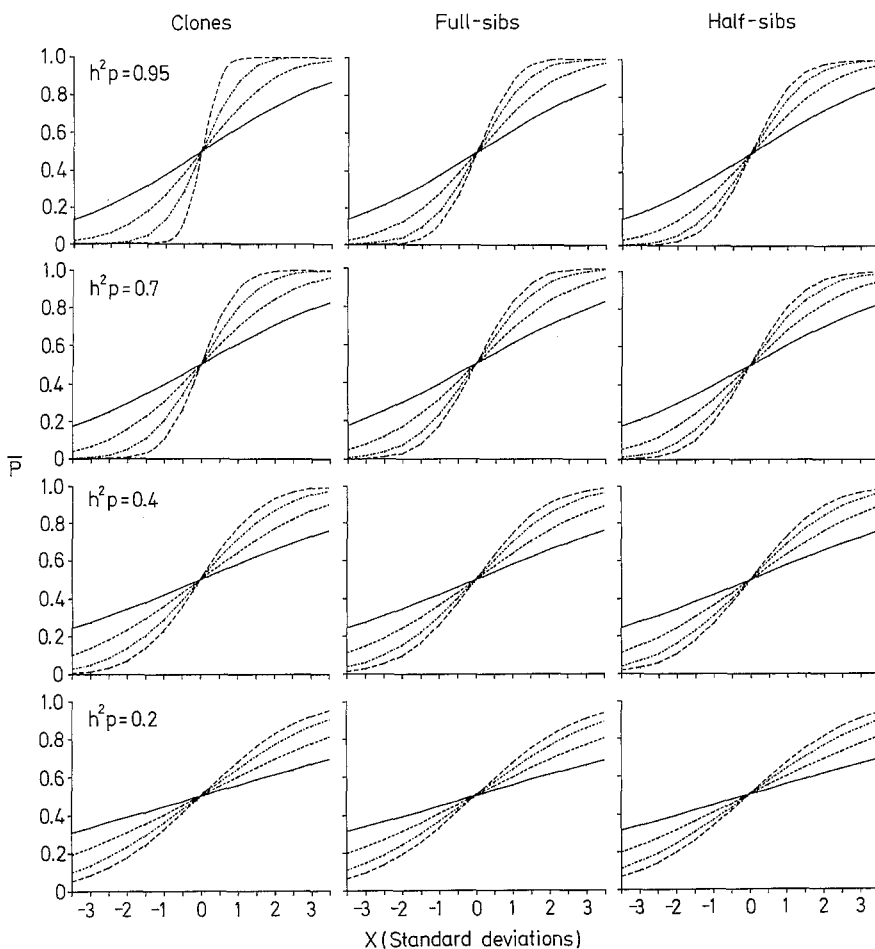


Fig. 1. \bar{P} (economic worth of 'off-spring') versus X with stepwise profit function [Eq. (15)] for clones, full-sibs and half-sibs; $h_p^2 = 0.95, 0.7, 0.4, 0.2$; h_o^2 (heritability in production population) = 0.9 (---), 0.6 (-·-·-), 0.3 (- - -), 0.1 (—). For $h_p^2 = h_o^2 = 1$ in the case of clones, the original profit function [Eq. (15)] holds

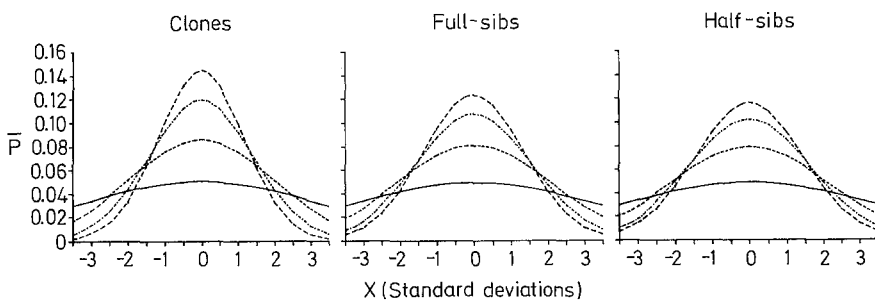


Fig. 2. \bar{P} versus X with normal-distribution profit function [Eq. (17)] and $h_p^2 = 0.9$ for clones, full-sibs and half-sibs, respectively; $h_o^2 = 0.9$ (---), 0.6 (-·-·-), 0.3 (- - -), 0.1 (—)

marginal worth for increasing metric value becomes negligible. Since the stepwise function [Eq. (15)] represents such an extreme case, the finding that a linear index is a good approximation with low heritabilities should hold well for almost any plausible monotonic function. Indeed, with many profit functions that are likely to exist, the finding should extend to appreciably higher heritabilities.

The normal-distribution profit function was chosen to address the case of where any departures from the crop mean tend to be adverse in themselves. Not only is it mathematically convenient to address but it also has an

economic plausibility. Obviously, the base-line could be set at other than zero economic worth – should it exceed zero, the relative advantages of clonal propagation could be reduced for given heritabilities, and if it were negative the advantages would be accentuated.

Genetic model assumed

An additive genetic model has been assumed. For clonal situations in themselves, it is immaterial to this study whether gene effects are additive or non-additive. In sexually produced offspring, however, non-additive gene ef-

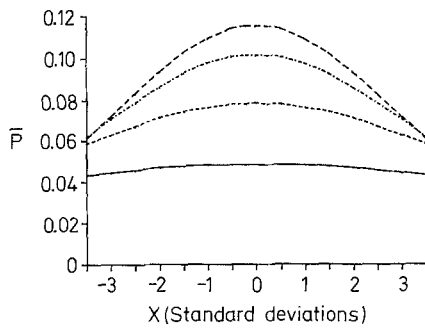


Fig. 3. \bar{P} versus X with normal-distribution profit function and $h_p^2=0.2$ for clones; $h_o^2=0.9$ (---), 0.6 (- · - · -), 0.3 (· · · · ·), 0.1 (—). Relationships for full-sibs and half-sib families essentially the same as shown here

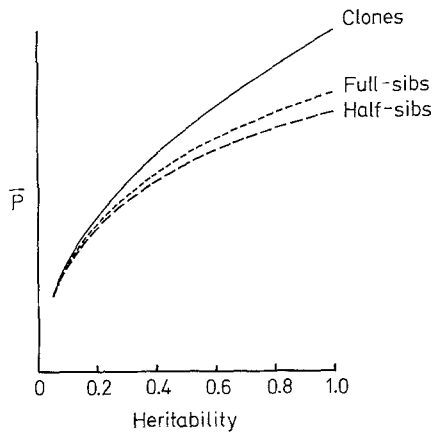


Fig. 4. \bar{P} versus h_o^2 with normal-distribution profit function with $h_p^2 \rightarrow 1$ and/or $n=1$ for clones (—), full-sibs (---), and half-sibs (- · - · -)

fects will make the appropriate heritabilities lower than those that would apply to clones. Hence, for a given candidate population, comparisons among clones and families for the impact of non-linearities in \bar{P} must, in effect, be based on lower heritabilities in the families. The full details of the comparative expectations are complex, but the consequent differences in the relationships will depend on the type of family involved (full-sib families differing from clones less than half-sib families), the magnitude of non-additive gene effects relative to additive ones, the nature of the non-additive effects (dominance or various classes of epistasis) and the mode of evaluating candidates (clonal tests, progeny tests or selecting individuals). These impacts depend primarily on the family coefficients of relationship being less for the various non-additive gene effects than for additive ones. Of course, if $\sigma_g^2 > \sigma_A^2$ (σ_A^2 = purely additive genetic variance), then clones have a theoretical advantage for any situation where directional selection is indicated.

Values of h_p^2 and h_o^2 can differ for various reasons. Where clonal or progeny tests are involved, h_p^2 will tend to exceed h_o^2 , hence the higher ranges considered for h_p^2 . For clonal tests, where genetic segregation does not arise, h_p^2 will tend to be higher than in progeny tests if test size is fixed, even with the purely additive genetic model.

General importance of non-linearities

The profit relationships have been studied over a range of 3.5 standard deviations of X about the mean in the parental generation (\bar{X}). This range embraces roughly the truncation points for 1:4500 selection for selecting clones or selecting prospective (full-sib) families on the basis of parental values ($\sigma_x^2 = \sigma_g^2/h_p^2$ in either case). For half-sib families ($\sigma_x^2 = \frac{1}{4}\sigma_g^2/h_p^2$), or full-sib family tests ($\sigma_x^2 = \frac{1}{2}\sigma_g^2/h_p^2$), this would represent much more intensive selection (It may be noted that while selection of individuals rather than clones or families, as such, may involve heavier culling, it will also tend to be associated with lower h^2 .) The implications of non-linearities, however, must be considered in the typical context of selection for several traits which are likely to have differing profit functions. For any one trait, given an appreciable intensity of selection, the candidates of serious interest can be expected to embrace only a limited part of the range of metric variation. Over such a limited range, the non-linearity will be less pronounced than over the total range. Selection intensities with respect to individual traits will not normally be particularly high, and occasional selections that are extreme with respect to individual traits are easily identified as such. It should be readily possible to infer whether the selection-index ratings in such instances would be seriously biased by non-linearities.

For many practical purposes the assumption of linear economic worth appears to be highly robust, at least where the profit functions are monotonic – indeed, to incorporate $P(y)$ directly in the index can grossly over-accommodate departures from linearity. In this light some of the selection index restrictions look questionable, despite their intuitive appeal. This is because most restrictions implicitly assume threshold effects for P in relation to X , which have been shown not to hold in the face of low heritabilities and genetic segregation if P values relate to individual offspring.

There is the question of how to cross-reference economic weights between traits with different types of profit function. Where quadratic functions are involved, some modifications of the Smith-Hazel solution, e.g. incorporating quadratic index terms (Wilton et al. 1968), use of square-root transformation of phenotypic values or use of partial derivatives of profit functions evaluated for expected means after selection [Itoh and Yamada 1988; Eq. (21)], can provide a quasi-linearity and meet the need for effectively different relative index weights according to

selection intensity. In fact, for the heritabilities and other conditions considered, the expected gains in efficiency relative to straightforward linear solutions were very minor, which accords with the results shown in Fig. 1. For more complex profit functions there seems to be no ready solution, and it seems appropriate to explore genetic gains under alternative index weightings and to translate them into economic returns under alternative selection intensities using Eq. (19). However, unless heritabilities are high and non-linearity is severe, the relative economic benefits in different traits can, for a given set of index weights, be essentially independent of selection intensity. This exploratory approach amounts to sensitivity analysis, which is advisable in any event for multi-trait selection.

The very marginal gains that would often accrue from explicit accommodation of non-linear profit functions must be viewed in the perspective of frequent uncertainties as to the relative economic weights among traits. More important, perhaps, than the fine details of optimising selection indices are the implications for integrating breeding and management for traits that show thresholds in profit functions. Where heritability is low, the scope for gains purely from genetic improvement is likely to be limited, unless selection is concentrated on the particular trait. Improved management practice then becomes doubly attractive, both to reduce directly the proportion of culls and to raise the 'offspring' heritability whereby the non-linearity can be expressed in \bar{P} and exploited.

Corrective mating can be used to achieve a desired X value using parents that diverge widely from it. The benefits depend strongly on \bar{P} values being higher for mid-parent X values than the average \bar{P} values for the disparate parents. This will, in turn, require certain types of non-linear profit function, e.g. intermediate optimum [Eq. (16)], law-of-diminishing-returns or stepwise [Eq. (15)]. However, it is clear from this study that the manifestation in \bar{P} of the benefits of non-linearity is strongly attenuated by both genetic segregation and low heritabilities. If the candidate population comprises inbred or strongly differentiated lines, then corrective mating can exploit favourable genetic dominance effect.

It is important to note that the profit function was deemed to apply at the level of individuals. Should it apply at the level of the population mean, the following equation obtains:

$$\bar{P} = P(y) \quad (y \approx h_p^2 X \sigma_x), \quad (21)$$

X being the phenotypic mean for the selections made in the candidate population. In this case, restricted indices and corrective mating would be far better based, since \bar{P} can show marked threshold effects with respect to X , even with low heritabilities and genetic segregation.

Note also that non-linearity of economic worth was considered in relation to traits that are economic in their

own right. This is not the same as when measured traits contribute non-linearly as components of economic traits, or when intercorrelations between different economic traits are inherently non-linear.

Implications for clonal populations

The advantages that can accrue from the genetic uniformity of clonal systems (or other systems based on genetic uniformity) clearly depend on high heritabilities, although for single-clone populations the heritabilities in the 'parental' material can become immaterial for the normal-distribution function. The advantages of uniformity fall into two categories. First, where an intermediate optimum exists, the genetic uniformity increases maximum economic worth of the population, particularly when broad-sense heritability is high (Figs. 2 and 4). (In fact, the advantage of clones should still hold for multiple optima, although it would presumably depend even more on high heritabilities.) Second, where profit 'plateaus' beyond a threshold value for the metric trait, an optimum economic worth with respect to that trait can be approached with a modest culling level, which would allow considerable scope for selecting for other traits before economic gains in the profit-threshold trait become significantly reduced. In this situation, sequential cutting or the use of independent culling levels could become very attractive relative to index selection.

The dependence of certain economic advantages of clonal systems on high broad-sense heritability has important implications for crop management. It places at a premium systems that minimise phenotypic variability between individuals. It fits, then, that clonal systems have found most favour under very intensive cultivation, where the crop environment is controlled so as to preclude most of the 'noise' variation.

Competitive influences, such as typically occur with canopy closure in a forest stand, can clearly amplify the plant-to-plant variation for growth variables. Where effects of genotype are being amplified thus along with those of environmental differences, the advantages of clonal systems are likely to become greater than have been indicated by the calculations reported here.

Conclusions

With heritabilities less than around 0.4, in either the candidates or the production population, the economic worth of 'parents' should closely approximate to a linear relationship with parental phenotype for almost any likely monotonic profit function relative to phenotypes of individual offspring – in most cases, the approximation would hold with appreciably higher heritabilities.

Where profit functions relate to individual offspring, the economic advantages of such features as non-linear

terms in selection indices, selection index restrictions, independent culling levels or corrective mating are likely to be very limited, except under high heritabilities and either clonal propagation or crossing between inbreds.

However, where the profit functions relate to the production-population mean, such departures from a linear index solution may be worthwhile, even with very low heritabilities and genetic segregation.

The economic benefits of genetic uniformity of clonal crops or crosses between inbred lines depend strongly on achieving high heritabilities within the production population.

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Appendix

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The solutions of Eq. (19) for the various profit functions [Eqs. (14)–(17)] are:

1. Linear [Eq. (14)]

$$\bar{P} = cy + q \approx cXh_p + q$$

2. Stepwise [Eq. (15)]

$$\bar{P} = 1 - F\left(\frac{d-y}{\sigma_y}\right) = 1 - F(S)$$

where $F(S)$ is the standardised normal cumulative distribution. $F(S)$ can be obtained from tables or calculated from approximation such as $F(S) \approx 1 - \frac{1}{2}(1 + 0.196854S + 0.115194S^2 + 0.000344S^3 + 0.019527S^4)^{-4}$ for $S \geq 0$; $F(S) = 1 - F(-S)$ for $S < 0$ (Abramowitz and Stegun 1970; Eq. 26.2.18)

3. 'Normal' [Eq. (16)]

$$\bar{P} = \frac{1}{\sqrt{2\pi(\sigma_y^2 + 1)}} \exp\left[-\frac{1}{2}\frac{(y-d)^2}{\sigma_y^2 + 1}\right]$$

4. 'Smooth' profit functions

$$\bar{P} \approx P(y) + \frac{1}{2}P''(y)\sigma^2$$

where $P''(y)$ is the second derivative of $P(y)$.

This is exact for polynomial $P(y)$ up to 3rd degree.

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