DEVELOPING BREEDING OBJECTIVES FOR RADIATA PINE IN NEW ZEALAND

C. J. A. Shelbourne
New Zealand Forest Research Institute, Private Bag 3020, Rotorua, New Zealand
L. A. Apiolaza
Department of Animal Science, Massey University, Palmerston North, New Zealand
K. J. S. Jayawickrama and C. T. Sorensson
New Zealand Forest Research Institute, Private Bag 3020, Rotorua, New Zealand

Abstract Selection indices for multi-trait and combined family and individual selection have been used in the New Zealand radiata pine breeding programme for the last 23 years, but no attempts have been made to formally develop a "breeding objective" in terms of the "aggregate genotype" (Hazel 1943). This programme has, until recently, focussed only on growth rate, form, and disease-resistance traits and a case is made for developing appropriate breeding objective(s), in response to present moves to improve wood quality and end-product traits.

Possible breeding-objective traits and their corresponding selection criteria are listed for all major wood products. Two high-level breeding objectives and their traits have been identified, but calculation of economic values of profitability have not yet been attempted.

These two main breeding objectives comprise the following traits:

- General Purpose—recoverable volume per hectare, adaptability, disease resistance, log quality (straightness and sweep), stiffness and strength as a plank, stability, mechanical performance (of clearwood).
- Appearance Grade Lumber—as above for General Purpose, except
  - without: stiffness and strength as a plank
  - with: appearance traits (resin pockets, blemishes, checking, colour, etc.) and maximum recovery of clearwood (from shop grades, factory grade, clear cuttings).

Keywords: aggregate genotype, breeding objective, end-product value, *Pinus radiata*, selection criteria, wood quality.

Background

Most of the theoretical basis for tree breeding derives from quantitative genetics as it has been applied in animal breeding. Following this model, M.D. Wilcox introduced the Smith-Hazel selection index to New Zealand tree breeding in the mid 1970s and these indices have been used routinely ever since, primarily as a tool to combine values of different traits that were measured or assessed in progeny and clonal tests (M.D. Wilcox unpubl. data; M.D. Wilcox, A. Firth, C.B. Low, and D. McConchie unpubl. data; Shelbourne and Low 1980). These indices were used for both selection on family means (for backwards selection of seed orchard parents) and for combined family and within-family, multi-trait, multi-site selection of individuals (forwards selection). The calculated index weights, however, were derived using arbitrarily allocated "economic weights" which, although they indicated some subjectively assigned, relative economic value of the different traits, had no real basis in the profitability or economic value of these traits. Our improvement programmes have been largely focussed on the growing of logs rather than on end-products and, like many users of selection indices in tree breeding, we made no attempts to formally define a "breeding objective", at least in the original sense of Hazel (1943).

However, this experience should be viewed in the context of the development and use of these concepts in animal breeding. Hazel and Lush (1942) for animal breeding, and also Smith (1936) for plants, independently proposed the idea of a linear function of recorded traits as a basis for selection, i.e., a selection index, but the key concept was Hazel's (1943) "aggregate genotype" or breeding objective, which is a combination of target traits, each weighted by their economic value or, as Hazel put it, "the amount by which net profit may be expected to increase for each unit of improvement in that trait". This is expressed by :

$$H, \text{aggregate genotype} = v_1A_1 + v_2A_2 \ldots + v_nA_n$$

where v_1, v_2 to v_n are the economic values and A_1, A_2 ... A_n are the additive genetic values of the various elements of profitability or "breeding objective traits".

The traits represented in the breeding objective should include all the main components of profitability of the whole production system. All components of the system need to be included, whether or not they are easily measurable or heritable. They are distinct from selection criteria (things that can be measured in progeny and clonal tests) (Clarke and Rae 1977; Ponzoni 1982) and recognising this distinction is a necessary conceptual step in defining a formal breeding objective.

The animal breeding literature, since the landmark papers of Hazel (1943) and Hazel and Lush (1942), is replete with papers on the merits and formulation of breeding objectives. Woolaston and Jarvis (1995) creditably bridge the gap between animal and tree breeding, and warn tree breeders of the critical need for formally defined breeding objectives for tree-breeding programmes. The distinction between breeding-objective traits and selection criteria has not always been clear to animal breeders, both for geneticists and producers (Barlow 1987; Ponzoni 1982; Ponzoni and Newman 1989; Harris and Newman 1994) and the confusion underlies much discussion in the literature. However, these and other authors, developing breeding objectives for different animals, all emphasise the fundamental importance of soundly based economic values for a formally derived breeding objective (Newman and Ponzoni 1994).

Many tree breeders have been unaware of these arguments, or ignored them, especially in programmes focussed on simple traits like growth and form. Yet for a species like radiata pine, which is processed into a number of different products of high added value, defining a breeding objective or different objectives for different product-related breeds is likely to be vitally important in planning the breeding programme. With a relatively long-lived tree crop such as radiata pine, selection of breeding population and seed orchard parents, or clones for deployment, is likely to be carried out on juvenile traits long before rotation age; thus the distinction between selection criteria and breeding objective traits is particularly relevant.

The only formally-developed and published breeding objectives in the tree breeding literature are the elegant work of Borralho *et al.* (1993) on alternative breeding objectives for kraft pulp production of *Eucalyptus globulus* in Portugal, followed by a similar study for *E. nitens* in south-eastern Australia by Greaves *et al.* (in press). Talbert (1986) set out the steps of formulating a breeding objective and selection index for tree breeding using a 10-year-old Douglas-fir progeny test example, and critically examined the selection index approach for a typical tree breeding situation with multiple traits, and with information from multiple relatives, and argued strongly in favour of the full breeding objective/selection index approach.

The goals of this paper are (1) to set out prospective breeding-objective traits that apply to each of the different classes of product, matching these with selection criteria that could be measured on younger trees in progeny and clonal tests, (2) to create one or more simplified breeding objectives that can be applied to different products, and (3) to indicate how these will fit into the breeding strategy. We do not attempt to formulate any economic values, v_n, in this paper, but this is a major and urgent task.

In the last 40 years, tree breeders have focussed largely on improving the growth and form of radiata pine through selection for diameter growth, bole straightness, branching habit, disease resistance, and freedom from malformation. Current problems with processing and marketing wood from fast-grown, intensively managed, shorter-rotation plantations have added impetus to a new thrust to genetically improve wood quality and thus end-product value (Sorensson *et al.* 1997; Shelbourne 1997). We need to properly formulate breeding objectives for these purposes.

Possible Breeding Objectives

Forest-growing objective traits

The profitability of growing trees is strongly affected by the survival, health, form, and growth rate of individual trees. These can be represented by the breeding-objective traits in Table 1, namely recoverable volume per hectare, adaptability, disease resistance, and log quality. Because establishment costs and silvicultural costs must be compounded to the end of the rotation, any factors affecting rotation length, especially growth rate, effectively control profitability of the forest-growing phase. However, variation in log quality and wood quality affecting product values are likely to have dominant effects on profitability of processing and marketing end-products. Improvement of end-product traits due to the value-added effect may have far more impact on total profitability than improvement of tree-growing traits (Shelbourne 1997), particularly for a vertically

TABLE 1. Breeding objective traits for different end-products of radiata pine in New Zealand

Forest-growing (all product objectives)
Recoverable volume per hectare
Adaptability to different environments (frost, nutrient deficiencies, wind-firmness)
Disease resistances (Dothistroma and Cyclaneusma)
Log quality (sweep, sinuosity, freedom from malformation)
Solid wood products
Appearance-grade lumber
Maximum recovery of clearwood (long internodes, unpruned logs)
Stability (on drying, remanufacture, and in use)
Mechanical performance of clearwood (stiffness, strength, hardness)
Appearance (freedom from resin pockets, checking, needle traces, and other blemishes; light colour)
Structural-grade lumber
Stiffness and strength as a plank
Stability (on drying and in use)
Mechanical performance of clearwood (stiffness, strength, hardness)
Poles
Taper
Straightness
Stability
Mechanical performance
Veneers
Knot distribution and size (clear or knotty grade)
Stability
Shrinkage (low radial and tangential)
Mechanical performance
Appearance
Reconstituted fibre products
Kraft pulp and paper
Pulp yield
Improved paper properties
Increased digester efficiency
Mechanical pulp and paper
Reduced power consumption
Improved paper properties

Note: Medium-density fibreboard, particleboard, oriented strand board, etc.: objective traits not yet definable (no individual-tree studies)

integrated industry. For the independent grower, the situation is different, yet unless his logs show improvement in end-product traits, they may sell poorly in a future, more-demanding market. However, we believe that modest further improvement in these forest-growing traits is still required for all breeding objectives and at all levels, from main breeding population to deployed families and clones.

Breeding-objective traits for different end-products

Breeding-objective traits are proposed in Table 1 for appearance grade lumber, structural grade lumber, poles, veneers, kraft pulp and paper, and mechanical pulp and paper.

Different end-products vary in their specific requirements and thus in potential breeding-objective traits, yet there is much commonality in many requirements. The most exacting product is appearance-grade lumber, where a long-internode branching habit in unpruned logs is needed to give high yields of the better shop grades (clearcutting grades), and various appearance characteristics such as resin pockets, needle fleck, and checking are important. Different breeding-objective traits are involved for reconstituted fibre products such as kraft pulp and paper but, as will be shown later, these can often be realised through selection for traits that will be required for solid wood products.

For all solid wood products, we see the wood characteristics of the corewood (that is juvenile wood within 10 to 15 rings from the pith) as being particularly deficient and thus a logical focus of genetic improvement. Overlaying all products and the development of breeding objectives is a need for uniformity. This implies uniformity within the tree as well as uniformity between trees of a clone, between members of a family and uniformity from site to site. Although it is possible to select for stability of performance across sites and for some reduction in within-tree gradients of wood properties, selection for within-family uniformity and against such biological gradients may prove ineffective. Dividing the new forest into single-clone units (or perhaps preselected, single-product, clone mixtures) is by far the most effective single step towards uniformity. Increased uniformity undoubtedly has a high economic value in this context and it must be included in considerations of profitability of breeding-objective traits.

Stability of boards or other solid wood products amounts to maintaining shape and size during processing, drying, reprocessing, and in use (B.G.Ridoutt and A.N.Haslett unpubl. data). This requirement for stability affects all solid-wood products, including appearance grades, structural timber, veneers, and even poles. Similarly, good mechanical performance of clearwood is needed for stiffness (modulus of elasticity) and strength (modulus of rupture) and often surface hardness for all solid wood products. The appearance traits, such as freedom from resin pockets, needle fleck, and other blemishes, and checking are of relevance to appearance-grade lumber and veneers only. Wood density and tracheid characteristics are important for reconstituted-fibre products (Uprichard *et al.* 1994; Kibblewhite and Shelbourne 1997), including kraft and mechanical pulp and paper, medium-density fibreboard, particleboard, and other panel products, and almost certainly will be found to be predictive of solidwood properties once the necessary research has been done.

Selection criteria for breeding objective traits

Most of the possible selection criteria that are related to the breeding-objective traits for each product are shown in Table 2. These relationships are often unconfirmed. Some are based on knowledge of clone-mean and phenotypic correlations from the studies reviewed by Shelbourne (1997) and which still need to be systematically reviewed and gathered together. In some cases, relationships are based on *a priori* reasoning and guesswork.

(1) Maximum recovery of clearwood

For appearance grade lumber, clear timber has higher value, with the long-length clears produced by pruning having the highest value. Trees with long internodes give high-value shop grades from unpruned logs; Beauregard *et al.* (1997) showed that large clonal differences in grade outturn of USA shop grades were largely dependent on internode index (proportion of clear lengths of 60 cm or greater).

(2) Stability

Most distortion of lumber on drying (instability) is due to irregular longitudinal shrinkage (Ridoutt and Haslett unpubl. data). Radiata pine normally shrinks about 2, 4, and 0.1% in tangential, radial, and longitudinal directions respectively. Distortion is caused by high spiral-grain angles (away from the longitudinal axis of the board) combined with high and/or irregular longitudinal shrinkage, which may be caused by compression wood with high microfibril angles (Harris 1977); compression wood can show up to 10-fold higher longitudinal shrinkage than normal wood. Differential shrinkage can also be due to variability in density within the piece as well as between latewood and earlywood within a single ring, especially for small components. The three key criteria relating to stability are therefore spiral grain, longitudinal shrinkage and compression wood.

Stability is also very important in structural timber and particularly so for veneers in both the longitudinal direction (in combination with grain angle) and in the radial direction (for rotary peeling) where variation in shrinkage leads to variation in thickness of veneers.

(3) Mechanical performance of clearwood

Stiffness of clearwood is generally lower for radiata pine than for many other conifers and particularly low for corewood (J.M. Harris unpubl. data; Walker and Butterfield 1996; Tsehaye *et al.* 1997). Two or even three-fold differences can be observed between the inner five rings and outerwood of trees of 35 years or older (H.R.Orman and J.M.Harris unpubl. data), and tree-to-tree variation in stiffness is poorly correlated with basic density. It is believed that improved stiffness of clearwood as well as strength and surface hardness are important breeding objective traits for all solid wood products. These characteristics are variously correlated with basic density, microfibril angle, and tracheid length (Bendtsen and Seft 1984) and quite probably with other tracheid cross-section dimensions, diameter, wall thickness, and wall area.

Selecting trees for clearwood stiffness of the corewood rings may prove to give higher gains and be more feasible than through correlated traits of density, microfibril angle, etc. (Tsehaye *et al.* 1997). Work is in progress at FRI to develop simple non-destructive techniques including using sonics, for measuring stiffness in small samples (R.E. Booker, pers. comm.).

Mechanical traits may also be related to other traits like pith-to-bark density gradient, ring width, and latewood percentage. Lignin content and composition and proportion of cellulose to lignin (e.g., high lignin in compression wood) may influence mechanical performance. These chemical characteristics are also economically important because of their relationship with pulp yield.

(4) Mechanical performance as a plank

Mechanical performance is a foremost requirement of structural timber where machine stress-grading is routinely used to record the minimum modulus of elasticity of a knotty plank. In the plank, stiffness and strength are affected by basic density and by size and distribution of knots as well as grain deviation associated with them. Clearwood stiffness is also evidently an important component of plank stiffness. Branch diameter and angle of insertion to the stem as well as internode length play an important part in stiffness as a plank, because long-internode trees have fewer larger branches.

(5) Appearance

Appearance traits, including resin pockets, needle fleck, and other blemishes, checking, etc., are components of a breeding objective for appearance-

TABLE 2. Selection criteria for breeding objective traits

Breeding-objective traits		Selection criteria (age 5–10 years)
Forest growing (all products)	Recoverable volume per hectare and adaptability to different environments	Diameter (dbh) Height Dothistroma score Cyclaneusma score
	Log quality	Straightness score Malformation score
Appearance grade lumber	Maximum recovery of clearwood (shop, cuttings, factory grade)	Internode index Branch habit score Branch index Branch diameter
	Stability *	Spiral grain (bark window) Spiral grain (core or disc) Longitudinal shrinkage Microfibril angle Compression wood %
	Mechanical performance of clearwood †	Stiffness (modulus of elasticity of bh clearwood) Strength (modulus of rupture of bh clearwood) Hardness (of bh clearwood) Basic density Density gradients (pith-to-bark, and intra-ring) Checking and collapse Tracheid length Microfibril angle Tracheid diameter (radial & tangential) Wall thickness Coarseness (wall area) Compression Wood Ring width Latewood percentage
	Appearance †	Resin pockets Heartwood Needle fleck Other blemishes Checking Colour
Structural grade lumber	Stiffness and strength as a plank	Internode index Branch habit score Branch index Branch diameter
	Stability	As for Appearance Grade
	Mechanical performance of clearwood	As for Appearance Grade
Veneer, plywood	Knot distribution and size (clear or knotty grade)	Internode index Branch habit score Branch index Branch diameter
	Stability	As for Appearance Grade Shrinkage (radial or tangential)
	Mechanical performance	As for Appearance Grade
	Appearance	Resin pockets Heartwood Needle fleck Blemishes
Kraft pulp and paper	Pulp yield	Pulp yield Lignin content Cellulose content
	Paper properties	Basic density Tracheid length Tracheid cross-section dimensions
	Increased digester efficiency	Basic density
Mechanical pulp and paper	Paper properties	Density Tracheid length Tracheid cross-section dimensions Stiffness Microfibril angle Cellulose content
	Reduced power consumption	Freeness (for given power)

* Assessable on small (30-mm-long) samples removed from clearwood at breast height.
† Assessable only by destructive sampling of internodal wood, and sawing.

grade lumber and veneers. Light colour and absence of resinous heartwood are additional appearance traits. Generally, but not always, the absence of appearance defects is considered desirable. Checking and collapse are problems affecting mechanical performance, as well as stability and appearance.

Machinability is a composite end-use trait related to grain angle, compression wood, earlywood-latewood density differences, ring width, and possibly some micro-anatomical traits. Treatability (penetration by different preservatives under pressure) is related to heartwood development and other factors. Gluability is also important to appearance grades in particular. The relationships of these possible breeding-objective traits with selection criteria need to be confirmed in any formal breeding-objective development.

(6) Kraft pulp and paper-pulp yield, paper properties, digester efficiency

Breeding objectives for reconstituted fibre products are process-specific. For kraft pulping, pulp yield (after digestion of lignin) is economically critical and sensitive to small improvements. Pulp yield is predicted by lignin and/or cellulose content. Paper properties are predictable from kraft fibre or wood tracheid dimensions and basic density (Kibblewhite *et al.* 1996; Kibblewhite and Shelbourne 1997). Wood density also controls the weight of wood for a given volume, which affects transport costs and digester efficiency, both economically important.

(7) Mechanical pulp and paper, power consumption, paper properties

For mechanical pulp, the objective includes improved paper properties and reduced electric power consumption in refining. Recent individual-tree and clone studies (Uprichard *et al.* 1994; Jones and Corson 1996) showed that, although there were large differences between trees and clones for pulping and handsheet properties, predicting these was less precise than for kraft. Also there are some contradictory requirements for basic density: low density gives improved tensile index and light scattering coefficient, and high density gives improved tear.

Proposed Simplified Breeding Objectives

There is evidently a high degree of commonality in requirements for different products, both in breeding objective traits and in corresponding selection criteria (Tables 1 and 2). If appearance traits, such as resin pockets, checking, and needle fleck, can be regarded as generally useful, there is only one real point of separation amongst all the objective traits and this relates to maximum recovery of clearwood (clearcuttings, shop grade, etc.), *v.* stiffness and strength as a plank. The former needs a long-internode tree with binodal or uninodal branching, and the latter a multinodal tree. It should be mentioned, however, that recent research (R. Beauregard *et al.* unpubl. data; D. McConnochie unpubl. data) casts some doubt even on this assumption.

One possible approach (Table 3) is to group the objective traits into two main breeding objectives called "general purpose" and "appearance lumber". Both focus on corewood characteristics, usually quite well-correlated with those of outerwood. The only salient difference would be in branch cluster arrangement, and this split could be made at the main breeding population level. Production population families or clones could be selected with specific economic weights on different traits according to their ultimate economic values in processing and products.

Breeding objectives should also be formulated for kraft and mechanical pulping. The former should include pulp yield, improved paper properties, and digester efficiency. However, this objective should be realised through similar selection criteria in the two main breeding objectives, which is appropriate where pulpwood derives from top-logs, thinnings, and slabwood from solid-wood crops. If and when pulpwood-only crops become feasible, they could be planted with clones or families with precisely specified wood and tracheid properties.

Breeding objectives for other products, including mechanical pulp and other reconstituted fibre products, need more research in identifying appropriate selection criteria. Increased cellulose content, reduced microfibril angle, increased stiffness, and increased wood density, all associated with the main breeding objectives, provide benefits for mechanical pulping (Uprichard *et al.* 1994; Jones and Corson 1996).

Breeding Objectives and Breeding Strategy

The New Zealand radiata pine breeding strategy has been described and developed progressively since the 1950s (Thulin 1957; Burdon and Thulin 1966; Shelbourne *et al.* 1986; Burdon 1988; G.R. Johnson and J.N. King unpubl. data; Carson *et al.* 1990; Jayawickrama, Carson, Jefferson and Firth 1997). The latest proposals of Jayawickrama *et al.* include a large main breeding population divided into two sublines, which supports and sources

TABLE 3. Simplified breeding objectives

Breeding objective traits		Selection criteria (all possible)
General purpose		
Recoverable volume per hectare and adaptability		Diameter (dbh) Height
Disease resistance		Dothistroma score Cyclaneusma score
Log quality		Straightness score Malformation score
Stiffness and strength as a plank		Internode index (low) Branch habit score (high) Branch index (low) Branch diameter (low)
Stability		Spiral grain (bark window) Spiral grain (core or disc) Longitudinal shrinkage Microfibril angle Compression wood (intensity and %)
Mechanical performance of clearwood		Stiffness (MoE of clearwood) Strength (MoR of clearwood) Hardness (of bh clearwood) Basic density Density gradient (pith to bark and intra-ring) Checking and collapse Tracheid length Microfibril angle Tracheid diameter (radial & tangential) Coarseness (wall area) Wall thickness Compression wood Ring width Latewood percentage
Appearance lumber—as for General purpose except:		
with:	Maximum recovery of clearwood (shop, cuttings, factory grade)	Internode index (high) Branch habit score (low)
	Appearance	Resin pockets Heartwood (none) Needle traces Blemishes Checking Colour (light)
without:	Stiffness and strength as a plank	

several small (24-parent) elite breeding populations (called "breeds") which comprise the best genotypes available for each breed. The "breeds" are selected for particular end-product or forest-growing roles and in which certain traits or trait groups are emphasised. There is an existing, modest-sized, long-internode breeding population, initiated in 1970, as well as other smaller elite populations for Dothistroma resistance and for high wood density. Three new elite breeding populations or breeds are planned, with threshold values for growth rate, form, Cyclaneusma and Dothistroma resistance, stiffness, and spiral grain.

The breeding strategies described above only attempted to improve some of the breeding objective traits listed in this paper. However, there are many possibilities for consolidating or diversifying objectives which can be done either at the breeding or production population level. Breeding-objective economic values for deployed clones or families could be "tuned" for different products or product lines, with special selection indices for these. The important thing is to quantify the relationships among breeding-objective traits and the numerous possible selection criteria, and then choose the best, most easily-measured predictors for operational use in the breeding programme.

The only real dichotomy in selection criteria and the related objective traits of "clears" *v.* stiffness-as-a-plank seems to come between the multinodal and long-internode branching habit (Shelbourne

1970; Jayawickrama, Shelbourne, Carson and Jefferson 1997). A long-internode branch habit is obligatory for production of appearance grade lumber from unpruned logs, but this material could arguably be used with appropriate stocking and silviculture in production of structural grade lumber, veneers, etc. Multinodal branch habit, on the other hand, is typical of most of the existing main breeding population and of present production population parent clones which have benefited from moderately strong genetic correlations between multinodal branching and diameter growth, and with bole straightness and freedom from malformation.

Incorporating several or many new wood and end-product traits, as well as traditional growth, form, and disease-resistance traits, into selections for the breeding population, or into families or clones for commercial planting, presents a major problem for the breeder. Finding parents or clones with even average levels of all desired traits and with higher levels for one or two requires exponential increases in population size, if the traits are uncorrelated. Relying on backwards selection of orchard parents amongst the few hundred progeny tested may be quite ineffective. Forwards selection in a large number of genetically diverse crosses, combined with cloning their offspring by a few ramets each, seems to be a way to precisely select individuals with the desired trait combinations. Many selection criteria, however, are likely to show positive genetic correlations, both amongst each other and with more than one breeding objective trait, which will facilitate multi-trait selection and improve the gains.

Concluding Remarks

We see the formal development of breeding objectives (*sensu* Hazel) as particularly necessary and timely at this stage in radiata pine improvement, where the direction is shifting from growth and form improvement benefiting the forest grower, to a much greater emphasis on improving end-product value for an integrated growing and processing industry.

The criteria for selecting parents for new breeds need more refinement and research. In particular, the covariance structures between objective traits and selection criteria, as well as their genetic parameters, need to be better established. Assessment of wood and end-product traits for genetic parameter estimation is very expensive, and offspring-parent regression offers a more precise method for number of families evaluated than sib analysis. Clonal experiments have proved their value in this respect.

The technology for measuring some of the selection criteria is also still being developed or the equipment is not yet available in New Zealand; for example, the sonic technique for clearwood stiffness, and SilviScan2 for tracheid cross-sectional dimensions, density, and microfibril angle. It seems likely that within 3 to 5 years good new techniques will be operational for non-destructive, reasonably priced evaluation of many of the selection criteria discussed.

With a species that is processed in many different ways, it will not be easy to calculate economic values of traits and develop formal breeding objectives. However, radiata pine breeders need to come to grips with economic value and profitability in the task of defining breeding objectives, something we have relegated to the too-hard basket for too long. We have been using selection indices for over 20 years and it is opportune now to properly apply Hazel's aggregate genotype concept in defining an economic basis for selection for breeding and deployment.

Acknowledgements The helpful comments on Tables 1 and 2 by the following are gratefully acknowledged: R.D.Burdon, M.J.Carson, A.N.Haslett, T.G.Jones, R.P.Kibblewhite, M.J.F.Lausberg, and J.G.Roper; many thanks also to R.D.Burdon for his editing and improvement of the manuscript.

References

Barlow, R. 1987: An introduction to breeding objectives for livestock. Pp.162–168 *in* Proc. 6th Conf. Aus. Assoc. of Anim. Breed. and Genet., Perth, W.A., Australia.

Beauregard, R., Gazo, R., Kimberley, M.O., Turner, J., Mitchell, S., and Shelbourne, C.J.A. 1997: Genotype variation in radiata pine random width board quality. *In* "Timber Management Towards Quality and End-Product Value", CTIA/IUFRO Internat. Wood Quality Workshop, Quebec City, Canada, 18–22 August.

Bendtsen, B.A., and Seft, J. 1984: Mechanical and anatomical properties in individual growth rings of plantation-grown eastern cottonwood and loblolly pine. Wood Fibre Sci. 18(1): 23–38.

Borralho, N.M.G., Cotterill, P.P., and Kanowski, P.J. 1993: Breeding objectives for pulp production of *Eucalyptus globulus* under different industrial cost structures. Can. J. For. Res. 23: 648–656.

Burdon, R.D. 1988: Recruitment for breeding populations: objectives, genetics and implementation. Pp.555-572 *in* Weir, B.S. *et al.* (Ed.) 2nd Internat. Quantitative Genetics Conf., Raleigh, N.C., USA, Sinauer Assoc., Sunderland, MS, U.S.A.

Burdon, R.D. (Comp.), and Thulin, I.J. (Ed.) 1966: The improvement of radiata pine. FRI Symposium No.6, Rotorua, N.Z.

Carson, M.J, Burdon, R.D., Carson, S.D., Firth, A., Shelbourne, C.J.A., and Vincent, T.G. 1990: Realising genetic gains in production forests. *In* IUFRO Working Party Meeting, Olympia, Washington, USA, August.

Clarke, J.N., and Rae, A.L. 1977: Technical aspects of the national sheep recording scheme (Sheeplan). Proc. N.Z. Soc. of Anim. Prod. 37: 183–197.

Greaves, B.L., Borralho, N.M.G., and Raymond, C.A.: Breeding objective for plantation eucalypts grown for production of kraft pulp. For. Sci. (in press)

Harris, D.L., and Newman, S. 1994: Breeding for profit: synergism between genetic improvement and livestock production (a review). J. Anim. Sci. 72: 2178–2200.

Harris, J.M. 1977: Shrinkage and density of radiata pine compression wood in relation to its anatomy and mode of formation. N.Z. J. For. Sci. 7: 91–106.

Hazel, L.N. 1943: The genetic basis for constructing selection indices. Genetics 28: 476–489.

Hazel, L.N., and Lush, J.L. 1942: The efficiency of three methods of selection. J. Hered. 33: 393–399.

Jayawickrama, K.J.S., Carson, M.J., Jefferson, P.A., and Firth, A. 1997: Development of the New Zealand radiata pine breeding population (in this Proceedings)

Jayawickrama, K.J.S., Shelbourne, C.J.A., Carson, M.J., and Jefferson, P.A. 1997: The long-internode breed of radiata pine—a case study of breed differentiation. *In* Proc. of 24th Bienn. South. For. Tree Impr. Conf., Orlando, Fl., U.S.A. 9–12 June.

Jones, T.G., and Corson, S.R. 1996: Relationships of TMP and wood properties of radiata pine trees. *In* Proc. 50th Appita Ann. Gen. Conf., Auckland, N.Z.

Kibblewhite, R.P., and Shelbourne, C.J.A. 1997: Genetic selection of trees with designer fibres for different paper and pulp grades. *In* Proc. 11th Fundamental Res. Symp., Cambridge, U.K.

Kibblewhite, R.P., Evans, R., and Riddell, M.J.C. 1996: Handsheet property prediction from kraft fibre and wood tracheid properties in eleven radiata pine clones. *In* Proc. 50th Appita Ann. Gen. Conf., Auckland, N.Z.

Newman, S., and Ponzoni, R.W. 1994: Experience with economic weights. *In* Proc. 5th World Congr. on Genet. Appl. to Livestock Production, Vol. 18, Guelph, Ontario, Canada.

Ponzoni, R.W. 1982: Breeding objectives in sheep improvement programmes. Pp.619–634 *in* Proc. 2nd World Congr. on Genet. Appl. to Livestock Production. Madrid.

Ponzoni, R.W.,and Newman, S. 1989: Developing breeding objectives for Australian beef cattle production. Anim. Prod. 49: 35–47.

Shelbourne, C.J.A. 1970: Genetic improvement of different tree characteristics of radiata pine and the consequences for silviculture and utilisation . *In* "Pruning and Thinning Practice", FRI Symp. No.12, 16–20 March 1970, Rotorua, N.Z.

Shelbourne, C.J.A. 1997: The genetics of adding value to the end-products of radiata pine (in this Proceedings)

Shelbourne, C.J.A., and Low, C.B. 1980: Multi-trait index selection of *P. radiata* progenies at five sites and associated gains. N.Z. J. For. Sci. 10: 307–324.

Shelbourne, C.J.A., Burdon, R.D., Carson, S.D., Firth, A., and Vincent, T.G. 1986: "Development Plan for Radiata Pine Breeding". Forest Research Institute, Rotorua, N.Z.

Smith, H.F. 1936: A discriminant function for plant selection. Ann. Eugen. 7: 240.

Sorensson, C.T., Cown, D.J., Ridoutt, B.G., and Tian, X. 1997: The significance of wood quality in tree breeding: a case study of radiata pine in New Zealand. *In* "Timber Management Towards Quality and End-Product Value", Proc. CTIA/IUFRO Intl. Wood Quality Workshop, Quebec City, Canada, 18–22 August.

Talbert, C.B. 1986: Multi-criterion index selection as a tool for operational tree improvement. Pp.228–238 *in* Proc. IUFRO Meeting, Williamsburg, Va. USA, September.

Thulin, I.J. 1957: Application of tree breeding to forestry in New Zealand. N.Z. J. For. 12: 41–46.

Tsehaye, A., Buchanan, A.H. and Walker, J.C.F. 1997: Selecting trees for structural timber. *In* "Forest Products for Sustainable Forestry", Proc. IUFRO Division 5 Conference, Pullman, Wa., U.S.A., July.

Uprichard, J.M., Kimberley, M.O., Foster, S., and Shelbourne, C.J.A. 1994: Thermomechanical pulping studies on ten *Pinus radiata* clones: the effects of wood quality on papermaking properties. *In* Proceedings of 1994 International Pan Pacific Conference, 6–9 November, San Diego, CA, U.S.A.

Walker, J.C.F., and Butterfield, B.G. 1996: The importance of microfibril angle for the processing industries. N.Z. For. 40: 34–40.

Woolaston, R.R., and Jarvis, S.F. 1995: The importance of breeding objectives in forest tree improvement. Pp.184–188 *in* "Eucalypt Plantations: Improving Fibre Yield and Quality", IUFRO Meeting, Hobart, Tas., Australia, March.