Branching habit in radiata pine - breeding goals revisited

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Abstract

Branching habit necessarily figures prominently in breeding goals for radiata pine in New Zealand. Past breeding has pursued two extremes of regular branch habit: what are effectively short internodes and long internodes respectively. The former, which has featured in the mainstream of the breeding programme, embodies indirect selection to control branch size and angle. However, it does not allow long clear-cuttings without pruning, unlike the latter. Despite much progress towards achieving these two ideotypes, the outcome has not been fully successful. The short-internode option has given insufficient control of branch size, while poor wood stiffness further downgrades the product for structural purposes. The long-internode option, pursuing 'uninodal' trees, allows quite long internodal clear-cuttings, but has shown even more than its anticipated drawbacks. Alternative ideotypes now proposed for providing internodal clear-cuttings have two co-equal branch clusters per annual shoot, over a considerable length of bole; branch clusters could be equidistant from each other, or else closely spaced towards the end of the annual shoot. Other possible ideotypes might be favoured for specific site types. Clonal forestry seems necessary to capture such ideotypes, and even then, capturing them poses major challenges. The ability to rejuvenate clonal material at will would be a very powerful tool for this, to avoid prolonged testing of huge numbers of candidate clones.

Background

Branch habit has figured prominently among selection criteria for breeding radiata pine in New Zealand. The species shows great variability in its branching pattern (Bannister 1962) - a tree can produce from one to five or even six or more branch clusters on a year's leader growth - and much of this variation is quite strongly heritable (Wu *et al.* 2008). Features of branch habit include: the frequency of branch clusters; their inverse function, namely 'internode' length; branch sizes; branch angles; and regularity of branching, in terms of both comparative lengths of different internodes, and the sizes and numbers of branches in neighbouring clusters. Of these features, branch cluster frequency/internode length is highly heritable, branch size much less so, and branch angle apparently in between. Heritability of components of regularity of branching has not been studied explicitly, but it would appear to be strong.

Accepting an **ideotype** as a set of attributes that embody an underlying breeding goal, we can define certain branching patterns as being likely to serve, at least in part, some diverse breeding goals for radiata pine. Two branch-habit ideotypes have been pursued in the past:

1. A regular, 'short-internode' or highly 'multinodal' habit; this is conducive to light, wide-angled branching, good tree form and rapid early growth, but incurs the penalty of allowing only short clear-cuttings between knot clusters unless the tree is pruned.
2. A regular, long-internode or nearly uninodal habit; this allows long clear-cuttings among knot clusters without pruning, but means large, steep-angled branches where they occur, and is liable to incur a significant penalty in terms of quality of tree form.

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Ideotype 1 was arrived at empirically, through finding that, on the pumicelands at least, the specification of light, wide-angled branching led to choosing strongly 'multinodal' trees. This empirical finding was reinforced by information on genetic parameters (Wu *et al.* 2008), namely variances, heritabilities and between-trait genetic correlations. Such information pointed to

- High heritability of branch cluster frequency (or 'internode length'), but low heritability of branch size.
- Strong genetic associations between high branch cluster frequency (short internodes), small branches (in relation to tree size), wide-angled branches, good stem straightness, low incidence of stem malformation, and good growth rate (at least in young trees).

As a result, branch cluster frequency (and, less formally, regularity of branching) became a key selection criterion for the 'mainstream' breeding programme, by virtue of its good heritability and the nexus of favourable genetic correlations with a number of other important traits. Indeed, this stands as a classic case of indirect selection. This emphasis on a short-internode ideotype had insistent support from industry (Burdon and Thulin 1966). Pursuit of this ideotype, having occurred de facto in making the '850'-series selections during the 1950s for the central North Island, became explicit in making the 268-series selections (in 1968) and their derivatives ('875' - and '880' series). It followed through into the main seed-orchard plantings and what was subsequently designated the Growth and Form (GF) breed. Subsequent offshoots of the breed have been the Dothistroma Resistant (DR) breed, and more recently, the Structural Timber breed (Jayawickrama and Carson 2000).

Despite the insistent industry call for the short-internode ideotype, there was concern among Forest Research Institute breeders in the late 1960s over a neglect of the option of a long-internode ideotype. Such an ideotype offered the prospect of quite long clear cuttings between knot clusters, without having to prune, although it was recognised that it would incur penalties (in terms of obtainable genetic gains) in respect of branch size and angle, growth rate, stem straightness, and malformation. Accordingly, a secondary breeding programme was set up to pursue this ideotype, seeking 'uninodal' or near-uninodal trees, which began with the '870' clonal series (Shelbourne *et al.* 1986). Provision for a seed supply was made in establishing the Tikokino Seed Orchard in Hawkes Bay, but demand for the seed was almost nil.

Selecting for the two extremes of branching habit had some additional, largely tacit rationales. It offered the prospect of minimising the incidence of a range of undesirable intermediate branch habits that one might expect from genetic segregation if parents of intermediate branching frequency were used. (The worst branching habit is clusters of large branches interspersed by closely spaced clusters of small branches, precluding good timber grades in unpruned logs for either structural or appearance products.) In effect, the dichotomy represented an attempt to achieve uniformity by using intense directional selection to 'squeeze out phenotypic variation against the end-walls of biological feasibility'. This was quite effective in itself. Another assumption, which was tacitly invoked for the mainstream programme, but not for the Long Internode breed, was that the favourable genetic correlations between a short internode habit and various growth and form traits were strictly linear.

In practice, selecting for the two extremes of branch cluster frequency was not a total success. The short-internode option has given less than the desired control of branch size (e.g. Carson 1988). In part, that reflects the adoption of silvicultural regimes that are far more radical, and shorter rotations, than what were envisaged when key breeding decisions were made (cf Sutton 2007), plus a shift towards planting more fertile, ex-pastoral sites. A lack of selection for wood properties, failing impetus from industry, has not helped. (Actually, effectiveness of selection for wood properties would have been limited by the role of microfibril angle in governing stiffness, and it would have been difficult to address stiffness except insofar as it is governed by density). On top of the failure of selection to improve, or safeguard, the quality of structural timber in the context, has been a loss of opportunities to obtain good-length clear-cuttings between knot clusters on unpruned logs. This has not been a problem with pruned butt logs, which have benefited from genetic improvement in growth and form (Carson 1988), but it has been particularly troublesome for second logs, which are too high to prune but too large to ignore, since these logs are not producing premium material for either structural or appearance grades.

The long-internode option, apart from an almost complete lack of market acceptance among forest growers, has had its own woes, over and above the anticipated penalties. On many sites, especially with fertility elevated by pastoral use, tree form is unacceptable. Moreover, the long-internode habit cannot be readily assured in the bottom 3 m of log in trees grown from seed (as opposed to cuttings with some maturation or 'physiological ageing'). Pruning of this part of the log would be indicated, especially as it produces wood of poor stiffness which would rule it out of high-value structural grades. The general observation that the long-internode habit is more satisfactory on some sites than on others implies that the strength of the adverse genetic correlations is site-dependent, being less with low-to-moderate site index and limited soil fertility and exposure. Some direct evidence for this has been obtained by Burdon *et al.* (1992b), while performance of different 'unimproved' regional stocks indicates that natural and silvicultural selection has led to a markedly more multinodal habit on the volcanic plateau, unlike in Otago/Southland (Burdon *et al.* 1997). Admittedly, there were impressive long-internode trees in the Kaingaroa 'old crop', but they were doubtless survivors of a high rate of suppression and/or malformation among long-internode individuals.

Concerns over pursuing extremes of branch cluster frequency have prompted several shifts in practice. In making the '885' to '887' plus-tree selections that sampled the remaining land-race material (Shelbourne *et al.* 1986), internode length ceased to be a selection criterion in its own right, although the large majority of selections made were markedly multinodal. In addition, the Long Internode breed has been redesignated the Clear Cuttings breed (Jayawickrama and Carson 2000), in recognition that a truly uninodal ideotype is on most sites unlikely to be worth pursuing seriously. Moreover, among clonal forestry programmes (e.g. ArborGen Australasia and Horizon 2, and Forest Genetics CellFor Ltd) attention is being given to the option of obtaining clear-cuttings, albeit as part of a clonal portfolio. Yet we do not appear to have a rigorous, basis for closely defining and capturing optimal ideotypes for obtaining clear-cuttings. That will require significant research.

Towards a new branching ideotype

It is suggested that the preferred ideotype for producing clear cuttings from a range of sites might be a regular binodal. Two versions of it could be:

- Two co-equal and equidistant branch clusters per annual shoot, giving two clear cuttings of around one metre,
- Two co-equal clusters, located close together (so as to represent a single short docking out) per annual shoot, giving a single longer clear cutting.

Of the two, the latter would likely be the more vulnerable to severe malformation consequent upon leader damage. Appropriate choice between these variants may well be site-dependent.

Such ideotypes are likely to be much more attractive if the genetic correlations between branch cluster frequency and various growth and form traits are inherently non-linear, in that any loss of genetic gain in growth and form traits, relative to a highly multinodal habit, would be very minor relative to the loss incurred by a uninodal (or near-uninodal) habit. This proposition is inherently testable, although a satisfactory test may not be straightforward.

In addition, given the effects of site on branching habit (Grace 2008), there may be sites where a truly uninodal habit is appropriate, on the one hand, or ones where three co-equal and equidistant clusters are appropriate, on the other.

With a branching ideotype designed to produce clear-cuttings, requirements for wood stiffness might be relaxed. How much they can be relaxed, however, may depend on interrelationships between stiffness and stability, since both these product-performance properties can be expected to be significantly influenced by microfibril angle (MFA) - high MFA is conducive to both poor stiffness and high longitudinal shrinkage, the latter being an important source of dimensional instability. However, reducing grain spirality would still be very desirable.

Towards capturing and growing new ideotypes

Capturing an ideotype in the middle of a wide range of genetic variation is not straightforward. With mass propagation by seed, genetic segregation can be expected to produce numerous genotypes (and thence phenotypes) that depart substantially from the intermediate ideal. Clonal forestry has obvious potential for capturing such an ideotype, because it avoids such unwanted genetic segregation among individual trees within the crop.

Practical difficulties, however, arise in capturing any proposed ideotype for producing clear cuttings between knot clusters. Within the tree, such a branching pattern should be repeated over a number of years, so it extends through several logs. This is an important complication because branch cluster frequency or, more specifically, internode length, tends to change significantly during the life of the tree (Grace and Carson 1993). Near the ground, the internodes (necessarily produced by the very young tree) tend to be relatively short. Then they usually become longer for a while, to become shorter again further still up the tree. The result is that internodes are usually longest in the upper half of the butt log and the second log. However, while average internode length for a population might show a relatively smooth trend with time, individual trees show a lot of obvious variation about such a trend. In any event, only a very small percentage of individual genotypes can be expected to show one of the proposed ideotypes over a long period, i.e., over a considerable height up the stem. That list of genotypes is likely to be shortened still further by immediate culling that can be done for wood properties, growth rate, and health traits.

Capturing such genotypes might be approached in two ways:

- **Selecting them from clonal tests.** This is likely to entail expensive testing of a large number of candidates, and to take quite a long time. These two considerations will place considerable demands on clonal storage facilities, unless cryopreservation is used, pending reliable results from clonal testing.
- **Capturing genotypes from ortets in plantations or progeny trials that have shown the desired, long-term ideotype.** This would require effective rejuvenation, to allow cheap mass-propagation; indeed, it generates a special attraction for being able to achieve rejuvenation in radiata pine. Not only would such trees display a desired ideotype, but their performance would be well replicated over time, although not over place. If such genotypes can be rejuvenated and propagated, they can still be tested as clones. Their juvenile performance, which tends to be characterised by developmental instability in radiata pine, will not have been well replicated over time (Burdon 1982), but in a clonal test it can be well replicated both among ramets per clone and across sites, and quick results can be expected for the key information.

Long-term replication over place is likely to be the missing component from such clonal evaluation. This may not be too crucial, however. Branch habit tends to become more heritable as trees get older (Burdon *et al.* 1992a). Moreover, rank-change genotype-environment interaction for branch cluster frequency evidently tends to be minor (e.g. Carson 1991; Jayawickrama 2001) but not always (Shelbourne and Low 1980; Kumar *et al.* in prep.). Nevertheless, there are questions as to what happens to the expression of an intermediate branch-habit ideotype over a range of sites. As site index drops, might the second 'internode' on the annual shoot get shorter? Or might there be some environmental threshold at which it just does not get produced? Making selections for such ideotypes locally could avoid such issues.

For addressing branch habit in the lower butt log (within 3 m from the ground) there are several options. In seedling material it is unlikely that the proposed ideotype is readily and reliably obtainable in this zone. This zone cannot be expected to produce good structural timber, because of its inherently low stiffness. However, it is easily pruned, and above it the clear-cuttings should be obtainable without pruning. If clonal material with some maturation is planted, the desired branch habit may be produced almost from ground level, but this would need to be substantiated.

Economic worth of a branch habit will depend largely on yields and lengths of clear-cuttings. However, it may also depend on the processing machinery available; in California, for instance, finger-jointing plant is attuned to the typical internode lengths of ponderosa pine.

How ill-suited a regular 'binodal' ideotype would be for producing structural timber is problematic. Much would probably depend on site, silviculture, and selection for wood stiffness.

Structural timber represents the high-volume Australasian market of radiata pine, and will doubtless remain the end-product for many growers. Nevertheless, appearance grades can command higher prices, with more global markets, while intensive pruning is a doubtful proposition for the long term. For many growers structural timber will remain the end-product, but high-quality, appearance-grade options are not to be passed up at all lightly.

Research matters

Research into branching ideotypes, as distinct from empirical selection and breeding, will not be straightforward. Characterising a branch habit entails achieving a quantitative description of:

1. Branch cluster frequency, in terms of mean internode length, or number of branch clusters per annual shoot,
2. regularity (or otherwise) of internode length,
3. range of branch sizes among adjacent clusters, and
4. vertical trajectories up the bole for each of the above (noting that there will be appreciable interdependences).

An ad-hoc integration of 1, 2 and 4 is effectively obtained in an Internode Index (e.g. Grace and Carson 1993), but it is essentially ad-hoc, rather than a basis for a truly rigorous characterisation of branch habit. Note that large branches (reflected in Branch Index) are not only undesirable in themselves, but strongly associated with undesirable features of steep branch angle. Other features of branching include numbers and size distributions of branches within clusters, and branch angles. The importance of such features can depend on the type of product being produced, but their value as additional information (and thence the need for data on them) may be reduced by strong correlations with more easily characterised features.

Finally, field performance and silvicultural needs of alternative ideotypes will need to be ascertained.

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