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Genotype × site × silviculture interactions in radiata pine: knowledge, working hypotheses and pointers for research§

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Abstract

Background: Favourable interactions between genotype, site and silviculture are desired for growing radiata pine, site and silviculture being two components of environment. Our challenge is to characterise the interactions so as to exploit them to advantage. Four classes of interaction are involved: three first-order interactions between pairs of factors; and one second-order interaction involving all three factors. Also of interest is to partition the interactions into two types: involving rank change of genotypes (RC interaction) and differing level of expression of genotypic differences among environments (LoE interaction).

Key issues: Tree breeders' immediate concern is with main effects of environment and interaction effects on genotypes' performance, yet prime interest for research and policy decisions lies in the role of environments and specific environmental factors in generating interactions. Of the two types of interaction, RC seems generally more important for breeding operations with LoE more so for deployment decisions.

Investigation: Existing information, and provisional expectations of interactions, is to be reviewed, mostly qualitatively, in terms of the comparative importance of RC and varying LoE. This will be done, for the first-order interactions, for various traits. Second-order interactions are as yet almost entirely conjectural. A framework is offered for accumulating both input from others and future research findings.

Key information: In radiata pine, growth traits, especially stem diameter, tend to show marked RC interaction with site. Tree-form traits, however, seem mainly subject to LoE interaction, and disease resistance is intensely so. Among wood properties, some show very little interaction, while LoE interaction seems to occur for some other properties.

Keywords: Genotype × environment interaction, Domestication, Genetic improvement, Deployment, *Pinus radiata*

Review

Introduction

In growing radiata pine (*Pinus radiata* D.Don), or any forest-tree crop, genotype, site and silviculture are key variables and are all central to the process of domestication. However, we cannot expect their effects to be straightforwardly cumulative; crop performance will doubtless be subject to interactions involving all these three classes of factor. Exploiting such interactions is being increasingly stated as an important goal for improving the productivity and profitability of commercial forestry in New Zealand. Studying such interactions, and thence understanding how they arise and can be manipulated, is a prerequisite for exploiting them. Thus, it is now, at the least, deeply implicit in Scion's research agenda, which includes a strong emphasis on boosting plantation productivity within the Growing Confidence in Forestry's Future (GCFF) research programme. Studying the interactions requires the establishment of a clear conceptual framework within which they can be researched, which we address below.

Before we address the conceptual framework for studying interactions in the forestry context, however, we briefly review two classic cases of interactions between genetic improvement and husbandry in the field

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of agriculture to illustrate how interactions can arise and be exploited.

The domestication paradigm

The domestication of plant and animal species has historically centred very much on exploiting favourable interactions between genetic improvement and management inputs, with domesticated stocks requiring but rewarding intensified management inputs. A classic example of favourable, synergistic interactions in plant breeding is afforded by the dwarf wheats of the “Green Revolution” which began in Mexico in the 1950s. These wheats could respond very well to increased fertiliser, with greatly increased yields (Borlaug 1970), whereas such fertiliser inputs made the more traditional long-strawed wheats prone to lodging which would vitiate their yield potential. (Admittedly, a question now exists over the long-term sustainability of such fertiliser use, but it is not seen as detracting from the illustrative value of this example.) In animal breeding, a good example exists in breeding for improved reproductive performance in sheep in New Zealand (Young 2015), boosting lambing percentages with twins and triplets instead of mainly single lambs. That can mean much improved meat production from the same, or even fewer, capital stock (see Figure 8 in Cocks and Brown 2005). But it does depend for its practical success on providing benign farm conditions with reliable and plentiful supplies of high-quality feed (Burton n.d.), so almost all the lambs can survive and prosper.

The conceptual framework

The conceptual treatment of genotype-environment interaction ($G \times E$) has been reviewed by various authors (e.g. White et al. (2007, pp. 134–140 and references therein)), but here, we extend it to partitioning environment into effects of site and silviculture, meaning three classes of potentially interacting factors, namely genotype, site and silviculture. This, in turn, means four classes of interaction, namely the three first-order interactions between pairs of factors and the second-order interaction involving all three factors. Not to be overlooked, however, are interactions that can arise just among the various site factors and even among silvicultural factors.

In traditional plant breeding, where interest lies in producing stable cultivar varieties, the focus has often been on the interactive behaviour of genotypes, especially stability of yield. From early days, a considerable literature has accumulated on yield stability analysis (e.g. Shelbourne 1972; Hill 1975), two alternative criteria being absolute stability and stability relative to the performance of the population of genotypes studied. With forest tree breeding, in which genetic gain is based on a platform of rolling population improvement, the appropriate emphasis is different. Paradoxically, although the breeder is interested in producing improved genotypes, the role (or roles) of environments in generating $G \times E$ is seen as being of prime interest to the tree breeder (Burdon 1977). The breeder has to choose screening environments for candidate genotypes and make selections among candidates on the basis of performance in the environments where they have been screened, and decisions arise in deployment of the select genotypes. All these processes will be most efficient in the light of knowing what performance in various environments tells us about the genotypes. What the tree breeder really wants to know is not only how the genotypes have performed in test environments but also how likely they are to perform how well both in any other sites in the forest estate and under alternative silvicultural regimes. Achieving that will depend on understanding the magnitude and types of interaction and how site and silviculture drive the interactions.

It is possible—and instructive—to partition $G \times E$ effects and variances into two component types, namely rank changes and level of expression (Dickerson 1962; Yamada 1962; Ding et al. 2008). The customary partitioning involves:

1) Differences among environments in the ranking of genotypes (RC interaction)
2) Variation among environments in the expression of genetic variation (LoE interaction)

For variances, this partitioning can be expressed as follows

$$\sigma^2_{GE} = \sigma^2_{GE'} + \sigma^2_{\sigma G} \tag{1}$$

where σ^2_{GE} denotes global $G \times E$ variance, $\sigma^2_{GE'}$ denotes the RC variance component and $\sigma^2_{\sigma G}$ denotes the LoE variance component, with σ^2_G denoting the genetic variance as expressed in an individual environment.

Such partitioning highlights two distinct, but not mutually exclusive roles of environments in generating $G \times E$, both of which are of interest for genetic improvement programmes. In practice, RC interaction is now customarily addressed in terms of departures from perfect linear genetic correlation between the performance of genotypes in different environments, a concept enunciated by Falconer (1952). Such correlation was termed type B genetic correlation (r_B) by Burdon (1977), $1 - r_B$ representing a measure of the extent of RC interaction. Such departures, it may be noted, can thus include curvilinearity which needs not entail changes in rankings; but such curvilinearity, while it may be of interest mainly for how it affects resolution of genotypic differences among the best genotypes (Burdon 1977), will not be discussed further. It is on the basis of r_B and its departures from +1 that RC interaction has been studied for radiata pine in recent years, being the focus of several major studies (e.g. Wu and Matheson 2005; Raymond 2011; Cullis et al. 2014; Gapare et al. 2015; Ivković et al. 2015; Li et al. 2015). Of these studies, all gave strong indications as to what factors were driving the RC interactions, except that of Cullis et al. despite the power of its factor analytic method for analysing a very large multi-site dataset with troublesome data properties.

By contrast, the LoE component has been subject to little if any formal study, although Burdon and Li[1] are currently simulating the potential impacts it has for some typical situations for breeding radiata pine in New Zealand.

In general, RC interaction tends to be of prime interest for breeding, for choice of screening environments and for genetic selection, whereas LoE is of interest more for deployment decisions. Its importance for deployment decisions has doubtless been grasped and applied intuitively by various tree breeders and forest managers, but a formal and explicit recognition and some quantitative analysis should provide a better basis for decision-making.

Studying RC interaction in terms of departures of r_B from +1 is based on treating the expression of each trait in each environment as a separate trait in its own right. That treatment can extend to the selection of genotypes or families that are replicated in different environments (Burdon 1979). But it can also be extended to coping with LoE interaction, because with LoE interaction, the effective economic worth of a trait can vary according to the environment. This can arise in several possible ways or situations. An obvious example is with disease resistance, for which genotypic differences in resistance will be of no economic consequence if the disease level is inconsequential. Another example is where the global economic-worth function for a trait may be curvilinear, while in some environments, the range of variation in the trait may fall within a 'plateau' domain of the trait, a situation that may well arise for some tree-form traits and wood properties in radiata pine on infertile coastal sands.

Both RC and LoE interaction can be readily accommodated, by treating the expression of each trait in each environment as a separate trait, in selection (Burdon 1979) as well as in research (Burdon 1977).

An alternative to Eq. 1 in partitioning of $G \times E$ variance (Muir et al. 1992) is into components that effectively involve differences among:

- Genotypes in ranking of environments, and
- Genotypes in expression of expression of environmental differences

While the latter may involve stability of the performance of individual genotypes, neither component is seen as being of pre-eminent research interest for the typical tree-breeding situation. Accordingly, this partitioning is not addressed further.

The stocktaking template

We plan to do a stocktake of $G \times E$ and collate it in a form that can be readily shared. This entails reviewing our knowledge, for individual traits of interest, of each class of first-order interaction (genotype × site, genotype × silviculture and site × silviculture) and, within each such class, known or presumed general magnitudes and comparative importance of RC and LoE interaction. In each case, we attempt to summarise quantitative evidence, and we list any known or presumed biological or biogeoclimatic drivers of interaction. However, we will generally avoid addressing the second-order interactions, while they remain largely conjectural.

Knowledge items to hand will be collated under the following categories and sub-categories

Class of first-order interaction

- Genotype × site
- Genotype × silviculture
- Silviculture × site

Then, for within each class:

Traits which may include:

- Height
- DBH
- Straightness
- Branching pattern (primarily 'internode' length or its inverse scale of degree of 'multinodality')
- Malformation (forking and significant stem deformation)
- General tree form (notably coarseness of branching as well as malformation)
- Wood density
- Stiffness (MoE, but low MoE likely associated with high longitudinal shrinkage)
- Other wood properties (e.g. resin pockets, dimensional stability, internal checking)
- Foliage diseases

Then, for each trait within each class:

Type of interaction (for each trait, in second column):

- Rank change (correlations) ('RC')
- Level of expression (general prominence) ('LoE')

Then, for each type of interaction, by trait, within class, indicate:

- General magnitude, reflecting $1 - r_B$ for RC interaction, roughly categorised where actual

estimates have been reported, as strong—r_B often <0.5, generally <0.66; moderate—generally $0.8 > r_B > 0.6$ and minor—$r_B > 0.8$
- Specific factors generating interaction, where interaction is appreciable
- Nature of effect(s) of each such specific factor, on mean (favourable or adverse) and on LoE (amplifying or diminishing expression of genotypic differences)

References will be denoted for each item of information. Presumptive information, in the absence of documented evidence, will be denoted as such.

The collated information will not be offered as definitive. Instead, we see it setting a framework for continual updating on the basis of input from others, and of fresh information, be it from references hitherto missed, personal experience or new experimental findings.

Note: Many entries, as they can be collated, will unavoidably be oversimplifications. Accordingly, anyone seeking guidance from individual entries will be strongly advised to consult the references cited.

Accordingly, we also request that any $G \times E$ information of the above types for radiata pine be sent for collation on Twitter <#GxSxSforests (see also Supplementary Tables S1, S2, and S3 in Additional file 1), seeking not only the genetic parameter estimates but also basic data and the available particulars on sites and silvicultural regimes. It is envisaged that the site can also be used as a chat room and that contributions all get due recognition. Despite our emphasis on radiata pine, corresponding information for other forest trees would also be welcome.

Interim evaluation of *G* × *E*

Pending a full literature survey, further analysis of existing data, fresh data collection and establishment of further field trials, we offer current perceptions of the nature and drivers of the various classes of interaction involving radiata pine.

Genotype × site

Rank-change interaction among genotypes (RC interactions) can be substantial in radiata pine for growth variables as shown previously by Fielding and Brown 1961, Burdon 1971, Johnson and Burdon 1990, Carson 1991, Jayawickrama 2001, Wu and Matheson 2005, Ding et al. 2008, Cullis et al. 2014, Gapare et al. 2015, Ivković et al. 2015, Li et al. 2015, Dutkowski et al. 2016 and in recent work by Li et al.[2] Most of the information is for stem diameter, which appears to show more such interaction than does tree height (Burdon 1971, 1976). Phosphorus (P) deficiency has in the past been strongly implicated as causing such interaction (Johnson and Burdon 1990 and references therein), but it is something that can be and generally is corrected readily enough. Other studies, generally conducted in contexts of using fertilisers where needed, have pointed to some different site variables as drivers of such interaction. Wu and Matheson (2005) pointed to altitude (elevation), as did Raymond (2011), whereas Gapare et al. (2015) pointed to temperature with a secondary role of humidity, Ivković et al. (2015) and Dutkowski et al. (2016) to rainfall and temperature, and Li et al. (2015) to mean annual temperature along with soil levels of nitrogen and total P. However, given the different sets of sites, and the auto correlations between site variables within those studies, there were probably no real inconsistencies among the findings. Also of interest would be interactions involving the 300 index (Kimberley et al. 2005) which is a measure of whole-crop productivity as distinct from individual-tree growth rate. However, while there is significant understanding of the site factors influencing the index (Watt et al. 2010 and references therein), there is little practical scope for studying RC interaction for the index at the level of individual genotypes. Competitive interactions among genotypes will make it very difficult to obtain reliable empirical information on interaction, except with blocks (simulating actual stands) of clonally replicated genotypes. That approach, however, will face difficulties in obtaining an adequate sample population of clones to give reliable information.

Foliage diseases, with individual genotypes differing strongly in susceptibility, are obviously subject to strong LoE interaction reflecting site differences in disease hazard which in turn typically reflect climate. However, such diseases can also generate strong RC interaction involving growth performance for genotypes among sites of differing disease hazard (e.g. Burdon et al. 1997; Dutkowski et al. 2016).

For wood properties (e.g. Burdon 1977; Jayawickrama 2001; Wielinga et al. 2009) and tree form (Jayawickrama 2001), RC interaction has usually been found to be minor, unless for instance if one is dealing with differential susceptibility of genotypes to pests or pathogens that affect tree form or wood properties. Severe nutrient deficiency can differentially affect wood properties among genotypes (Burdon and Harris 1973), but badly affected genotypes would contribute little if anything to crop yields, meaning that such interactions may have virtually no practical importance.

Interaction of the LoE type can also be strong, where sites differ strongly in P deficiency (Fielding and Brown 1961; Burdon 1971, 1976) or in foliage disease hazard (although P deficiency is becoming irrelevant because of how easily it can now be corrected). The role of disease hazard here is self-evident, but main interest will lie in cases of disease levels that favour identifying the most resistant genotypes. However, LoE interaction tends to be very strong for straightness, malformation and coarseness of branching and possibly wood stiffness. For tree-form traits, the LoE interactions can often be stark, in which on some sites, form can be almost uniformly good whereas on others, it varies widely about an average of bad to very bad. Nevertheless, the evidence tends to be anecdotal, because practical necessity means such traits are typically rated in genetic trials subjectively, with the rating scales not being absolute. The main factors involved, which have generally adverse effects and strong expression of genotypic differences, include high soil fertility and exposure. A notorious, if ill-documented, example exists in the grossly inferior tree form of long-internode genotypes (of low branch cluster frequency) compared with short-internode material on very fertile sites, especially if they are severely exposed. Among wood properties, compression wood incidence, which is seen as a driver of dimensional instability, has been shown to exhibit LoE interaction (Burdon 1975). In the apparent absence of specific documentation, the expectation is that high fertility would be associated with greater expression of genotypic differences in stiffness, and dimensional instability associated with longitudinal shrinkage and grain spirality, in addition to generally adverse effects. For the secondary wood property, resin pocket incidence, genotypic differences will almost certainly be much more strongly expressed on high-hazard sites which are in some degree identifiable (Cown et al. 2011 and references therein), although evidence of the heritability of resin pocket incidence is largely lacking.

Genotype × silviculture

The RC interactions among genotypes that result from differing silvicultural regimes are generally thought to be minor (Waghorn et al. 2007; Laserre et al. 2009; Lin et al. 2013, 2014). However, there are doubtless effects like control of foliage diseases being able to alter genotypic rankings on sites of high disease hazard or correction of *P* deficiency affecting rankings.

The LoE interactions involving different expression of genotypic differences according to silviculture can be major, partly insofar as silviculture may modify site properties. While generally not explicitly documented, such interaction can doubtless involve some tree-form variables, notably incidence of malformation and coarseness of branching. Wood properties that are likely to be similarly involved are stiffness and dimensional stability. The main silvicultural factors involved include low stockings (including heavy thinnings) and boosted soil fertility, which have generally adverse effects on these variables along with presumed elevated expression of genotypic differences.

Silviculture × site

While no explicit published documentation has been found, site differences are not generally believed to have major effects on the rankings of silvicultural regimes in respect of the tree variables we have considered. However, sites can have major effects on differences among silvicultural regimes. On sites that are very fertile and/or exposed, the differential effects of silvicultural variables can become drastic. Low stockings can have disastrous effects on malformation rate, coarseness of branching and wood stiffness (and probably grain spirality) on such sites. Strong effects on means for tree-form traits may be associated with amplified expression of genotypic differences (LoE interaction), although there may be extreme combinations of site and silviculture in which tree form is almost uniformly disastrous.

Genotype × site × silviculture

While the second-order interactions are still largely conjectural, there appear to be synergistic effects between, soil fertility and exposure (both site factors), and genotype, these site factors often amplifying the expression of genotypic differences. Returning to the case of long-internode genotypes showing very poor tree form on sites that are very fertile and/or exposed, low stockings will almost certainly have a synergistic effect, making the situation even worse. A similar synergism likely involves poor wood stiffness (and longitudinal shrinkage), also at low stockings on sites that are very fertile and/or exposed. In such cases, expression of genotypic differences may be amplified, in LoE interaction, by these site and silviculture factors. However, if a combination of these site and silviculture factors means that all genotypes cause almost uniformly disastrous tree form, there would be LoE interaction suppressing effective expression of genotypic differences.

Addressing second-order interactions will be challenging. It will likely begin with visualising and formulating potential interactions, followed by generating and testing hypotheses concerning the nature and drivers of the interactions. Testing the hypotheses and generating new ones, however, will surely be helped by the large volumes of new types of data that can now be collected using remote-sensing and new laboratory-assay technologies.

Pointers for further research

The proposed collated information will serve to highlight uncertainties and thereby provide pointers for further research. A careful stocktaking and prioritising of these uncertainties is certainly indicated. In some cases, the entries in the database may suffice to prompt searches of existing reports (including unpublished findings) that will plug knowledge gaps. In other cases, a resulting awareness of knowledge gaps may prompt fresh assessments of existing field genetic trials, or appropriate trawling of New Zealand's Permanent Sample Plot database, may serve to plug gaps. In yet other cases, however, fresh field trials may need to be established.

Importantly, in analysing both RC and LoE interaction, it is advantageous to treat the expression of each trait in each environment as effectively a separate trait.

Whatever the comparative importance of RC and LoE interaction, the tree breeder would want to identify the environmental factors that drive $G \times E$. That should make it possible to identify and choose a small subset of test sites on which good performance of candidate genotypes would assure good performance anywhere in the forest estate that is served by the particular breeding programme. It applies whether the breeder chooses to select for 'stable' genotypes that perform well throughout or for different sets of genotypes that perform best in particular situations, a topic of perennial debate discussed by Li et al.[2] Characterising the roles of particular environmental factors in generating $G \times E$, though, is very challenging. While some consensus is emerging in respect of radiata pine (Raymond 2011; Gapare et al. 2015; Ivković et al. 2015; Dutkowski et al. 2016) and in recent work by Li et al.[2], the task is much complicated by several factors, notably: poor genetic interconnections between different existing field trials, high degree of autocorrelation among various climatic factors and even between climatic and soil factors, the diversity of potentially relevant soil factors and imperfections in soil assays as proxies for relevant biological factors. Thus, we are far short of having any general understanding of the quantitative drivers of genotype × site interactions. However, information on the interactions involving silvicultural factors may provide helpful insights as to the drivers of $G \times E$.

Combining information from various sources will pose numerous challenges and will ideally require various items of information not listed in the template we have offered. Statistics from various sources will vary widely in precision, raising weighting issues; information will be available for various tree ages; genetic populations involved will vary; age-age and between-trait genetic correlations may vary among sites and silvicultural regimes, creating additional categories of $G \times E$; even silvicultural regimes are defined by multiple variables; and experiments have often lacked the statistical power to give good information on possible divergences between $G \times E$ involving additive and non-additive gene effects. However desirable it may be to devise and optimise quantitative algorithms combining such information items in order to achieve a synthesis, it seems unlikely that judgement art can ever be fully supplanted by rigorous science.

Conclusions

In radiata pine, growth traits, especially stem diameter, tend to show marked genotypic RC interaction with site. Tree-form traits, however, seem mainly subject to LoE interaction, and disease resistance is intensely so. Among wood properties, some show very little interaction, while LoE interaction seems to occur for some other properties. Despite some leads, information is very incomplete on the environmental drivers of genotype × site interaction. Also, very incomplete is information on various interactions involving silviculture. The key to understanding the second-order, genotype × site × silviculture interactions is seen as first obtaining a good picture of the three classes of first-order interaction, in terms of both RC and LoE, for the economic traits, with respect to the specific factors generating the interactions. Achieving that is an ongoing task, which will entail progressive accumulation and synthesis of information from the efforts of various teams of researchers. Understanding the interactions is important for evaluating candidate genotypes, deployment of selected ones and matching management practices to deployed material.

Endnotes

[1] Burdon RD and Li Y (in prep.). Genotype-environment interaction involving site differences in level of expression of genotypic variation: simulations to explore economic significance.

[2] Li et al. (in prep.). Genotype by environment interactions in forest tree breeding: review and perspectives on research and application.

Additional file

Additional file 1: Three tables listing known or postulated first-order interactions involving genotype, site and silviculture in radiata pine. These show provisional information, and as such are offered as the framework for updating, through further collation of existing literature, fresh data analysis, and fresh experimental work. **Table S1**. Known or postulated genotype × site interactions in radiata pine, in terms of role and effects of site on expression of genotypic differences for specific tree variables (Carson 1989; Kumar and Burdon 2010). **Table S2.** Known or postulated genotype × silviculture interactions in radiata pine, in terms of role and effects of silviculture on expression of genotypic differences for specific tree variables. **Table S3.** Known or postulated silviculture × site interaction in radiata pine, in terms of how impacts of site factors on means and expression of differences for specific tree variables are affected by silviculture (lower stockings/heavier thinning regimes, or fertiliser use). (DOCX 33 kb)

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Authors' contributions

RDB drafted the manuscript and finalised the revision. The remaining authors have contributed through collaborations to the ideas for this paper and to its revision. All authors read and approved the final manuscript.

Competing interests

The authors declare that they have no competing interests.

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