Genetic aspects of risk - species diversification, genetic management and genetic engineering

Rowland D. Burdon

Abstract

The topic is addressed in terms of (1) risk profiles (2) the types of risk management measure taken: risk avoidance, risk spread, and response preparation (3) types of risk to be addressed: biological and market (4) the levels in a genetic hierarchy at which measures are taken: species, provenances, breeds, individual genotypes, and individual genes. Within this framework, and the context of available or potential propagation technology, the New Zealand situation is reviewed, with emphasis on what types of measures are being applied at what level in the hierarchy and how they are integrated. The present approach centres mainly around risk management within the context of the *Pinus radiata* species monoculture, and is addressed with special reference to biological risks such as the arrival of a new and serious disease. Several lines of defence exist, with short-term defences involving a combination of risk avoidance and risk spread, and longer-term measures involving mainly response preparation. Recourse to other species, as ‘contingency’ species, fits mainly as response preparation. An integrated system is mostly in place, based on the combination of genetic material and propagation technology. Concerns exist, however, over: response preparations on contingency species; devising and implementing risk-spread codes for deployment practice; and the commercial stands being effectively excluded from the genetic material for response preparation. New biotechnology, involving specific genes, at once provides a risk management tool and yet poses its own risk management issues.

Introduction

Risk management is not a new theme in New Zealand forestry. It has been implicitly addressed, at the generic level, both in the long-standing debate on species diversification and in species siting. The debate, however, has been rather intermittent, and it focuses on only one genetic aspect of risk management. In recent years species diversification has been addressed in various documents, generally in relation to the radiata pine monoculture (e.g. Burdon 1982; Sweet and Burdon 1983; Burdon and Miller 1995). Nowhere, however, do the genetic aspects of the topic appear to have been addressed within a full conceptual framework. That I will attempt.

Five aspects to consider are:

- risk profiles
- types of risk management measure
- types of risk to be addressed
- genetic levels at which the management is addressed
- specific risk management measures

I will examine the first three individually. I will then consider the final two together, to examine the historical implementation and the way in which risk management measures are (or are not) currently embodied and integrated in New Zealand forestry practice and research.

Risk profiles

A risk profile is the relationship between the probability of loss (or performance below expectation) and the magnitude of the loss. Typically it represents a distribution characterised by relatively high probabilities for low levels of loss, through to much lower probabilities in the region of catastrophic losses - except with an obviously dangerous practice when there will be high probabilities of even serious losses. The effective magnitude of economic loss may not be in simple direct proportion to the physical loss. For example, while minor losses may be readily tolerated a threshold may be reached beyond which the operation, and even dependent communities, will cease to be economically viable. Such relationships, however, will depend strongly on the wider context of risk spread. In any case, risk is effectively a function of the probability and the seriousness of an eventuality.

In practice, the risk profiles are often poorly known. At one extreme, we have a reasonable quantitative picture of wind-damage hazards, and a good idea of various predisposing factors, although the impact of tree breeding on susceptibility to wind damage is unknown. At the other extreme, we have very little actuarial base for defining risk profiles for serious diseases, with much of the uncertainty arising in the level of seriousness in the event of the disease arriving. Obviously we do not want to go through accumulating a precise actuarial base, so we must be prepared to live with major uncertainty. An intermediate case would involve insect pests of eucalypts in New Zealand, which affect groups of species, and are arriving at what is now a predictable rate, albeit with uncertain impacts.

Type of risk management measure

Three major categories may be recognised: risk avoidance, risk spread, and response preparation against eventualities.

Risk avoidance

Risk avoidance can entail what could be termed ‘passive’ and ‘active’ measures. Passive measures generally embody a conservative pursuit of gain where a close positive relationship is perceived between expected rate of return and level of risk. Active measures to counter risks can be exemplified by breeding for disease resistance; that, however, will have its costs, not only in the resistance breeding but also in opportunity costs with respect to breeding for other traits. In any event, empirical field testing of material must remain a prime
tool for risk avoidance, although there are ancillary methods of evaluation. Such evaluation, however, has its limitations, resulting from the practical difficulties of extrapolating performance in time and across sites.

**Risk spread**

This is exemplified in diversifying species on the supposition that, while each may entail certain risks, the probability of simultaneous evanescence of the risks for all the species is lower than for the risks associated with any one species. This in turn requires that the risks concerned are essentially independent or, better still, negatively interdependent. Appropriate patterns of risk spread can depend very much on the geographic range and scope of operations of the party concerned. Take two contrasting cases, both illustrating risk spread. At one extreme, a small woodlot on a farm would represent a minor risk exposure for the farmer concerned. At the other extreme, an entire New Zealand operation could represent a only a minor risk exposure for a large transnational.

Here we have an issue that pervades New Zealand forestry: whether the total forestry-related risk exposure for communities, and even the national economy, may become excessive despite the individual 'players' having satisfactory risk spread for their own business interests.

**Response preparation**

This involves being prepared to take corrective action only after an eventuality. In effect, it amounts to devising contingency plans and setting them in place. It depends on the conditions that, on the one hand, the various costs of other types of risk management measure are unduly high in relation to the perceived risk profile and, on the other hand, that rapid and effective post-hoc responses are feasible. At the highest level, this approach may entail being prepared to turn to other species. At a lower level, it may entail having select clones in reserve which can be mass-propagated at short notice. It thus requires whole packages to be in place, not only having genetic material available and readily identifiable as appropriate, but also having the means of rapid deployment. The latter entail having adequate seed sources available, or else the vegetative propagation technology and the requisite logistical systems.

**Types of risk**

The more tangible risks fall into two broad categories, biological (including bioclimatic) and market risks.

Biological risks in the narrow sense include fungal diseases, insect damage, and other animal damage. In a broader sense, since species, provenances and individual genotypes can vary in susceptibility, biological risks can also include climatic damage, the principal agents in New Zealand being wind and snow, with frost and/or drought being locally significant. Insofar as susceptibility to fire can be a feature of species it could even rate as a biological risk. Risks of climatic damage can generally be addressed by risk avoidance, in choice of species and species siting and, to some extent, by choice of provenance. So can risks of existing diseases. Risks of new or unknown diseases, however, are less readily combated in this way.

Market risks centre mainly around the inevitable uncertainties of future markets. That is somewhat distinct from the differentiation of species according to suitability for different end uses. The risks can be addressed in different ways, either by trying to produce general-purpose wood, or by a 'portfolio' approach. Under the latter, differentiated categories of material are produced, in the hopes that one or more categories might command a high value for market niches, while the remaining categories, through being well characterised, should command adequate returns. Siting practices, silviculture and rotation length, however, are additional tools for addressing market risks. In general, however, achieving market flexibility entails markedly higher effective growing costs (Grant 1976).

Far less tangible, but potentially very serious for forestry, are risks relating to public perception. These can arise in external perceptions of what is technically or environmentally sound, or ethically acceptable; they involve issues such as the rights and wrongs of species monocultures, clonal forestry or genetic engineering, or even cultural sensitivities. Public-relations disasters, once incurred, are very hard to rectify.

**Genetic levels and specific measures for addressing risks**

These levels come in the order of levels at which genetic improvement needs to be addressed:

- species
- provenances within species
- breed differentiation
- individual genotypes and,
- with the application of new biotechnology specific genes.

**Species**

In the first planting boom of 1925-35, after the major commitment was made to Pinus radiata, the Forest Service practised active species diversification, which was partly linked to species siting. Four plantation species were mainly used: P. radiata, P. ponderosa, Douglas-fir and Corsican pine (P. nigra var. laricio), with significant areas of some other species such as P. contorta, P. muricata and P. strobus. Later on, significant areas were planted with P. taeda, P. elliottii and P. patula. In hindsight, this pre-emptive diversification was largely a failure, in both risk avoidance and risk spread. Also the opportunity costs were huge, because the 'other' species were so much less profitable than P. radiata. In terms of risk avoidance, the use of P. nigra and P. ponderosa, which had been seen as biologically 'safer' and better timbers than P. radiata, failed badly. Both species were much more affected by Dothistroma needle blight. In utilisation, P. ponderosa was much inferior, and even P. nigra had no decisive advantages and some disadvantages. Douglas-fir, while much more expensive to grow, has advantages in resistance to damage from wind and snow, but it can suffer from Swiss needle cast and sometimes from defoliation by insects, and is highly vulnerable on frost flats. It has an advantage in respect of market risks, with a different end-use profile, al-
though achieving a high value premium depends on accepting high effective growing costs. Thus there were huge departures from the classic relationship between risk and potential returns.

With the outstanding economic advantages of \( P. \) radiata and its general adaptedness, the use of other species has offered little in both risk avoidance and risk spread, on both the biological and market fronts. Thus the main thrust of genetic risk management must be within this species (Burdon 1982; Sweet and Burdon 1983). For a fall-back position, several species must rate largely as 'contingency' species (Burdon and Miller 1995). If they are to figure in the risk management scheme that must be on the basis of response preparation. That preparation entails:

- ascertaining what species should be used, either as pure species or hybrids, on what sites, in the event of a biotic crisis (e.g. a new and very serious disease) ruling \( P. \) radiata out from much of its present range in New Zealand. This in turn entails confirming growth performance, site tolerances, tree form, health, and acceptability of the wood, all relative to other candidate species;
- securing of good seed sources, or else acquiring other adequate genetic material together with reliable technology for mass vegetative propagation, in order to allow a very rapid shift to the contingency species.

While details of the utilisation would remain to be sorted out, the major effort would probably be needed only after a commitment was made to a species.

From the late 1960s, after it became clear that Dothistroma blight was less than catastrophic, and until very recently, no grave biotic threat to \( P. \) radiata was seen within the sector, although western gall rust and possibly pine nematode were seen as potentially serious should they arrive in New Zealand. No serious corporate commitment to the issue of contingency species was forthcoming in this period; indeed, an attempt to sell this as a priority research topic to a Research Advisory Committee in 1980 was firmly rebuffed. At that time this would have reflected disbelief that any grave biotic threat to \( P. \) radiata existed, more than any belief that the only thing making plantation forestry worthwhile in New Zealand was \( P. \) radiata.

In the last few years, however, pitch canker has emerged as a new threat because of its impact in the native stands (Storer et al. 1997). It has claimed attention in New Zealand, and reminds us of the potential menace of western gall rust.

Considering contingency species as pure species, preparations are very incomplete (Burdon and Miller 1995). While we generally know what provenances we would use for species that might replace \( P. \) radiata, do we not fully know what species would be preferred on what sites in lieu of \( P. \) radiata. While the existence of seed sources has been monitored, systematic forward planning for seed sources of alternative species went effectively into abeyance for over 10 years and has only been reactivated in the last two. Provision for keeping forest statistics for monitoring the existence of plantations that could serve as future seed sources also lapsed in large part. The Public Good Science Fund has until very recently been providing considerable funding for research on 'alternative' species, but that is not addressing contingency species as such. Monitoring and replacement of genetic resources of alternative species has not yet caught up again, and will remain an ongoing need.

The species with which \( P. \) radiata can hybridise are few. They do include at least two that are quite resistant to pitch canker but have important drawbacks. And it should be readily possible to develop mass-propagation technology for the hybrids. Thus such hybrids have possibilities as contingency material in the medium term, and some hybrid seed involving more resistant species has been obtained within the sector.

Even with a diversity of species, the use of species monocultures, i.e., pure, even-aged stands of single species, disturbs many of the public. However, apart from the huge practical difficulties and opportunity costs of managing mixed stands of our exotic species, there is the fact that monocultures often mimic the natural regeneration ecology of the species (Burdon 1982).

**Provenances**

Here risk avoidance is almost paramount in risk management. While the provenances of fastest growth and best form may be sought, there is the need to assure adequate site adaptation and wood properties. In Eucalyptus nitens, for instance, the higher growth potential of the central Victorian provenances compared with those from New South Wales can be mitigated on warmer sites by disease susceptibility. In Douglas-fir there remains the question of whether the very fast-growing provenances, from the coast of California and Oregon, are appropriate for our high-altitude sites where Douglas-fir would be preferred to \( P. \) radiata.

Within \( P. \) radiata, choice of native provenance is, for various reasons, a far lesser issue than for some other species. Nonetheless, the Guadalupe provenance has promise as a source of resistance to western gall rust (Burdon 1992). Moreover, even a less promising provenance can show some unexpected resistance to a biotic hazard, as with the resistance to the Cambaria provenance to the root pathogen Phytophthora cinnamomi in Western Australia.

**Breed differentiation**

A feature of New Zealand's Radiata Pine Breeding Programme is that the improved genetic material is being differentiated into a number of distinct "breeds" (Jayawickrama and Carson (in MS)). This is a response to a combination of: the diversity of end-uses, the diversity of sites where the species is grown, and the highly plastic behaviour of the species (e.g. variation in tree form and wood properties) according to site conditions. Different subdivisions of the breeding population, within which the continuing improvement
over successive generations is achieved, are aimed at different breeding objectives which are encapsulated in the breed names: Growth and Form (the original 'mainstream' breed, with a strongly 'multinodal' branching habit), Dothistroma Resistant (an early offshoot of Growth and Form), Structural Timber, and Clear Cuttings (to partially supersede the old Long Internode breed). This differentiation has been achieved mainly by selecting from within the local stocks of the species, but drawing from specific native provenances can enhance the process, as with using some trees from the Guadalupe provenance for Structural Timber.

This differentiation of breeds, and their deployment to sites, addresses all main aspects of risk management. Specifically, the Dothistroma Resistant breed is about avoiding (or countering) a biological hazard, but there can be elements of avoiding both market and biological risks in the siting of some other breeds. Regarding markets, the diversity of breeds stands to have a strong element of risk spread, as well as an important historical element of response preparation in the partly superseded Long Internode breed.

Individual genotypes

The tree-to-tree genetic variation is not just a platform for both selective breeding and breed differentiation; it is also a key to both risk spread and response preparation. Using a multiplicity of unrelated clones (or of seed-orchard parents) for the commercial stands that are being established, is a risk-spread measure, protecting the forest grower against adverse genetic sampling error with respect to susceptibility to a hitherto unknown risk factor (say, a new disease). For instance, while any one genotype may be especially susceptible, it is most unlikely that a number of unrelated individuals from the same population would all be so susceptible. The expected standard deviation of the mean susceptibility of a set of clones, for instance, will decline according to the inverse of the square root of the number of clones; for example, the standard deviation among the means for sets of 100 unrelated clones will be one-tenth of that among individual clones. For a disaster threshold, with a given probability that any one clone is affected, the probability that any particular number out of a set of clones will be simultaneously affected is given by a simple application of the binomial theorem. Thus, for four clones, each with a probability of disaster of 0.1, the respective probabilities are 0.66, 0.29, 0.05, 0.004 and 0.0001 that zero, one, two, three or all four clones would be affected. The probability of all clones being simultaneously involved is a function of the probability of a single clone being affected to the power of the number of clones; thus if the probability for any one clone is 0.12 that for all four clones of a group being similarly affected is 0.124 = 0.0002. Robards and Bishir (1997) concluded that 30-40 unrelated clones give essentially all attainable risk-spread protection against catastrophic failure.

Other factors may have to be considered. A mix of clones can, depending on the biology of the pathogen, confer some epidemiological protection against disease over and above the protection afforded by risk spread. In practice, increasing the number of clones will generally entail a significant sacrifice of potential genetic gain. Indeed, if that entails compromising the general level of adaptation it may lead to some loss of field resistance to pathogens in general. I concur that, on balance, the risk spread achieved is typically of very little net value beyond 20 clones or so, with 40 being a very generous figure.

Considerations for the number of seed-orchard parents are basically similar. However, the process of seed production releases genetic variability which is expressed even among seedlings with both parents in common. Intuitively, this would tend to reduce the requisite numbers of orchard parents relative to the requisite number of clones for clonal forestry. Yet the appropriate relaxation of requisite numbers is likely to be only marginal.

Some code of practice seems appropriate, to govern the effective numbers of clones (adjusting census numbers for unequal representation), or effective numbers of orchard parents, used for establishing plantations within given geographic units. Any such code must accommodate several considerations: the level of commitment to the species concerned (which will define the level of ultimate risk spread), the relatedness among material deployed (which will require upward adjustments to numbers used), the degree to which existing clones or orchard parents for production populations will be replaced over time with their own relatives, and the pattern of deployment (mosaics of monoclonal stands or mixtures of clones). While it is possible, in principle, to grow mixtures of clones that are very similar for economic traits, monoclonal stands may still have important advantages for silviculture and utilisation. Final choice of pattern of deployment may therefore depend on factors like whether commercial thinnings are planned and the logistical feasibility of arranging salvage fellings of blocks of individual clones.

Prescribed minimum numbers of clones to be deployed in plantations have been imposed by law in some European countries. These minima are as high as hundreds in some cases, which is quite unrealistic. Yet if the industry in New Zealand fails to police itself in this respect, and be seen to do so, it may both lose public confidence and be saddled with undue restrictions. The task, however, may be much complicated by over half the planting now being done by the 'small players' rather than the large corporates which are well placed to implement codes of practice.

Forward preparation at the level of individual genotypes can take several forms. Tested material can be held in reserve. More positively, select material can be screened for resistance to dangerous diseases that might arrive, such as the testing of select New Zealand material in California for pitch canker resistance.

For the longer term, genetic resources are potentially crucial. In the short term, with stands that are being planted, one can prepare for the unknown es-
sentially by risk-spread measures. If only 5% or less of the population shows worthwhile resistance to a new disease, that will not really help in current stands. For the future, however, a very low incidence of adequate resistance may still allow successful breeding for resistance, provided the genetic material has been managed properly. In fact, our "production populations" which generate commercial stands are underpinned by the larger and more genetically diverse breeding population. In turn, the breeding population is underpinned by the still larger and more diverse gene resources, which used to represent our local, unimproved stocks but now represent collections of native-population material growing in some of our forests. This hierarchy of populations (Burdon 1997) reflects the trade-off between level of genetic improvement and genetic diversity. The material in reserve represents lines of defence by virtue of a range of propagation technology that allows rapid multiplication of commercial stock from new selections. Another feature of the scheme, for which there are several reasons, is having commercial stands a genetic dead-end, which effectively relieves the forest grower of responsibility in genetic management beyond the deployment of improved commercial material. This, however, may be a serious drawback for coping with the contingency of there being rare genes of large effect being crucial for conferring resistance to a new and serious disease (Burdon 1997), a phenomenon which has been observed in western North America. This problem may be most acute for large-scale clonal forestry. Thus, to take risk management really seriously, the forest growers may need to deploy material in ways that allow commercial stands to help provide the genetic back-up, like how dairy herds now serve as production and breeding populations. The technical and logistical challenges (Burdon 1997) would be major, and a severe test of political will.

Specific genes

Classical breeding work involves half the genes of a parent going to each offspring. Where a highly specific attribute is sought from an outside source, e.g. another species, the desired genes (which are usually not recognisable as such) typically come with many unwanted ones. With annual crop plants this can be overcome with generations of backcrossing into existing varieties, but this approach is generally prohibitive with forest trees. New biotechnology, however, makes it possible to recognise and even incorporate single genes that are desired for specific purposes. And such genes can come from well beyond the limits of crossing compatibility.

At one level, it is becoming possible to use genetic markers to identify particular chromosome sites that govern large gene effects. With time it will become possible to identify individual genes that are responsible. Much more radically, the use of genetic engineering will allow the introduction of specific genes. Such technology could serve either risk avoidance or response preparation by introducing specific disease resistance, according to whether the disease is already present or not. Conferring resistance in this way may provide very important back-up for natural resistance.

Yet the same technology has its own risks (Burdon, in press). Admittedly, several widely-publicised risks are non-issues in New Zealand plantation forestry, because foodstuffs are not produced, our species are exotics with no native relatives, and there is a sharp division into plantation forestry and native wildland management. Even so, pollen shed by 'transgenic' trees remains a concern. Also, single genes conferring resistance to diseases or pests can be 'defeated' by adaptive shifts in the pathogens/pests, requiring multi-gene control to assure durable resistance. This may be of little concern if the disease affects only juvenile trees; otherwise, it may carry the less obvious danger of the disease striking after species sitting has been based on resistance that proves non-durable. Other risks include side-effects on field fitness resulting from either the process of gene insertion or side effects of the action of introduced genes. Serious side-effects are unlikely, but they cannot be ruled out. One possibility, for which there is indirect precedent in maize, is a dramatic loss of resistance to a disease strain that may only materialise after a number of years. Given the rotation span of many forest trees the consequences of such a development could be dire. Empirical testing of transgenic material will therefore greatly reduce the risks, but this will take time and will never be quite complete. Time will reveal the true risks, but on present knowledge an elaborate scheme of risk spread among genes inserted and insertion events seems indicated, even after a period of testing.

The regulatory machinery in New Zealand poses a problem, because the HSNO Act which governs the release of genetically-engineered organisms has no provisions for imposing any risk management conditions upon approval of commercial releases. However, this problem is recognised and should be rectified long before commercial releases are sought.

Concluding remarks

The genetic aspects of risk management cannot be considered in isolation from other aspects. Silviculture can be a powerful tool, and can interact strongly with genetic improvement. Of special note, however, are the potential bad interactions between quarantine and genetic measures in risk management. Quarantine is often crucial, even if only to buy time. But it can also, if applied over-zealously, prejudice access to genetic material of high value for risk management. And it can be counterproductive in other ways. For instance, New Zealand's internal Dothistroma quarantine restrictions were, in hindsight, futile in themselves and considerably hampered the delivery of genetic gain through seed orchards.

We have a considerable genetic risk management strategy in place, with a number of lines of defence and of technology pathways. Yet I see some weaknesses, especially in response preparation. These in-
volve preparation gaps with contingency species, and the current exclusion of improved, commercially deployed stocks from the scheme of long-term genetic management. The present commercial and institutional environments create some strong disincentives for forest managers to address these gaps or to have them addressed, but the gaps will not disappear spontaneously. In addition, an explicit risk-spread code is needed for field deployment practice. New biotechnology, like most new technologies, is at once both a tool for addressing risks and a source of new risks. The new risks pose challenges, but should be manageable if duly recognised.

Finally, the genetic aspects must be considered in the total context of risks. Trying to reduce genetic risks to zero may be futile if there are appreciable geophysical risks, e.g., of large pumice eruptions. The latter risks, however, will argue for a geographic risk spread in location of genetic material.

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References