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Conservation and management of potentially resistant tree germplasm: a key but easily neglected part of a robust biosecurity strategy[†]

Rowland D. Burdon

Scion, Private Bag 3020, Rotorua 3046, New Zealand.

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rowland.burdon@scionresearch.com

Abstract

A comprehensive biosecurity strategy must contain due provision for living with uncontained incursions of injurious organisms. Collectively termed pests, these organisms include fungal pathogens and certain insects. Provision for living with such pests includes availability of genetic material that offers pest resistance. For that, genetic diversity is a widely agreed requirement, especially as pests can appear with no prior record of being significant.

While breeding for resistance is a rear line of defence, it poses a special need for forward preparation. Maintaining and structuring the appropriate genetic diversity, however, can be very challenging. Genetic improvement of preferred species can accentuate their preferred status, making it even less attractive to retain stocks of potential back-up species. And in the preferred species, genetic improvement can escalate the opportunity costs of retaining unimproved or less-improved material containing much more genetic diversity than the main commercial crops. Also, importing fresh germplasm poses some border security risks. Furthermore, globalisation compounds certain institutional factors that militate against retaining genetic diversity.

These issues particularly affect countries where commercial forestry depends on exotics. New Zealand is a notable example. About 90% of its commercial forest estate is in one greatly preferred, exotic species, *Pinus radiata* (D. Don). This species is the subject of intensive genetic improvement, which has very strong industry uptake, while it is widely grown on sites of relatively high disease hazard. Stringent quarantine and general regulatory restrictions greatly hinder the importation of fresh germplasm. Other complications include: global interests and strong international risk spread of foreign forest owners; and rapid changes in forest ownership and management. Unfortunately, the current Ministry of Agriculture and Forestry Forest Biosecurity Strategy does not really address forward provision for breeding for resistance. A solution must be multi-pronged, with commitment from various parties.

Keywords: biodiversity; biosecurity strategy; genetic resources; resistance breeding; risk management.

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Introduction

Biosecurity strategies rightly have a strong focus not only on border control but also on the measures and organisations to contain and suppress incursions of injurious organisms (pests) that will occur despite the best efforts of border control. Even so, some of the incursions will prove impossible to contain, so a truly robust strategy must include provision for living with the uncontained incursions.

Various tools exist for living with pests (both pathogens and animal pests) when once they have become established. The tools are best used in some combination, under the term Integrated Pest Management. That can include: use of fungicides or animal poisons; manipulation of silvicultural regimes; more specific forest hygiene measures; and use of genetic resistance, which will be my focus.

Using genetic resistance will depend on the availability of genetic diversity with respect to resistance. Such diversity can exist at any level in the population hierarchy:

- among species (which have their own hierarchy of taxa);
- among populations within species; and
- among individuals within populations (be the populations natural or synthetic).

Use of resistance can entail direct use of innately resistant species, or populations within species, but it can also be based on actual breeding for resistance. Breeding can be based purely on selection to exploit differences among individuals, but it can also entail hybridisation between populations or distinct species. If the pest involved in the incursion is known to be significant, or potentially so, there may be pre-existing knowledge of the patterns of genetic diversity for resistance at the various levels in the population hierarchy, involving the geographic distribution of resistance and the level and nature of individual-tree variation. Such knowledge can guide the choice of material to select and deploy in order to minimise the impact of a pest. In the absence of the pest, however, the incentives to apply such knowledge by securing and/or conserving and managing resistant (or potentially resistant) material can easily be insufficient to ensure appropriate action.

In fact, history teaches us that troublesome pest incursions typically do not involve known hazards. Instead, they have tended to come from 'left field'. A century or so ago, chestnut blight (caused by *Cryphonectria parasitica* (Murrill) Barr) (Smith, 2000) and white pine blister rust (caused by *Cronartium ribicola* J.C.Fischer) (Hunt, 2003) were inadvertently

imported from the Old World, where they were not serious pathogens, into North America. There, chestnut blight has been totally devastating, and blister rust has caused serious and widespread mortality. Around, 1960, *Dothistroma septosporum* (Dorog.) M.Morelet (previously identified as *D. pini* Hulbary), which had been known as only a minor pathogen, started to strike exotic pine plantations, including plantings of *Pinus radiata* D.Don (Burdon, 2001a). This happened in East Africa, Hawaii, New Zealand, Chile and Australia, as well as in *P. radiata* planted north of its natural range on the Pacific coast. Indeed, *D. septosporum* rapidly eliminated *P. radiata* as a species option in many parts where it had hitherto thrived. Other pathogens have also affected *P. radiata*, either as new arrivals within the species' natural range or as essentially unknown pests affecting exotic plantings. Pitch canker, caused by *Fusarium circinatum* Nirenberg & O'Donnell, while recognised as a problem in southeastern USA, made a very unwelcome appearance in California in the mid-1970s (Storer et al., 1997). Since then, *Neonectria* [syn *Nectria*] *fuckeliana* (C.Booth) Castl. & Rossman has appeared as a troublesome pruning-wound pathogen in New Zealand (Dick et al., 2006) with no known record as a significant forest pathogen; and *Phytophthora pinifolia* sp. nov. has similarly appeared in Chile, as a cause of alarming needle cast and some shoot dieback (Durán et al., 2008).

Clearly, specific knowledge of requisite pest resistance is widely lacking. Some pointers, though, do exist as to how best such diversity might be sought. Comparisons between planting sites and natural habitats of commercial species can indicate likely vulnerabilities. For instance, fungal diseases are a likely hazard where a species (or a provenance) is being grown in habitats wetter than those of its natural range, especially if summer rainfall is prevalent. Conversely, insect pests are a likely hazard on sites hotter and/or drier than the natural habitats, although they are evidently more amenable to biological control than are fungal pathogens.

These elements of predictability will apply mainly to species and to a lesser extent populations thereof. Such predictability, however, may not extend to hitherto unrecognised pests. Within populations, genetic diversity tends to be essentially random, and can best be sought in numbers, supplemented by the best available estimates of the level of individual-tree variability. Effective population size, namely the equivalent of the number of unrelated individuals, which can be inferred from a known pedigree structure, is the key to retaining pre-existing variation. In practice, sheer numbers of individual genotypes, the less interrelated the better, offer the best prospect of retaining the genetic diversity that is available within populations.

Preservation of genetic diversity has been addressed

in the context of managing native species (Schaberg et al., 2008), usually growing within their natural ranges. Concerns have arisen over the potential erosion of genetic diversity through heavy thinning of stands or the use of scattered seed trees for natural regeneration. I venture that, at least on the landscape scale, this is likely to be a non-issue; because the allele losses that might occur would tend to be very localised and made good by the gene flow that typically occurs. But, should a native species become intensively domesticated, with an ill-conceived breeding programme, such concerns could become valid.

With countries that grow exotic species, however, the situation can be very different. There can be several factors:

- prior to the establishment of certain pests or pathogens, the role of climate in favouring such organisms can be masked (cf. Liebhold et al., 1995); thus there could be explosive epidemics of freshly arrived pests in crops that had hitherto thrived;
- the genetic base, and thence genetic diversity, of the tree species can be restricted for historical reasons;
- such species can be subject to intensive genetic improvement which is conducive to narrowing the genetic base;
- species that are not of prime economic interest can be neglected or even largely eliminated; and
- exacerbating these various problems can be institutional factors, regulatory restrictions, and public policy positions.

These issues are highly relevant in New Zealand, which provides a case history that should have important lessons for various other countries with major commitments to exotic forestry.

The New Zealand Context

New Zealand is a classic case of a country with a major commercial forestry sector that is based almost 100% on exotic plantations. Moreover, roughly 90% of this plantation area is occupied by a single, greatly preferred species, *Pinus radiata*, a circumstance that has changed little in the last 30 years or so. Also, this species has been subject, since the early 1950s, to a large and intensive breeding programme (e.g. Burdon et al., 2008), which has given substantial genetic gains and received very strong uptake from industry. The degree of genetic improvement already achieved has enhanced profitability. Yet it has created some

problems, through greatly increased opportunity costs of retaining and managing genetic resources that represent lower or zero genetic improvement. These resources are still valuable, however, as they offer greater variability than is represented in the intensive breeding operations. Such resources, in the case of preferred species, can include much larger populations than those involved in the breeding programme and/or natural populations that have been represented little if at all in generating domesticated stocks. The resources, however, can also include stocks of species of purely contingent interest for commercial forestry.

Despite its greatly preferred status, growing *P. radiata* does involve significant biotic risks. There is the inherent risk that an exotic species is growing in environments where some pest(s) not yet present could run rampant. Such pests, we now know, can include ones both native and non-native to the tree species' natural range. In addition, we know that the species is widely grown on sites that, while inherently productive, pose elevated biotic hazards because of the amount of summer rainfall (Burdon & Gea, 2006).

The hazards of growing exotics in the absence of certain pests were dramatically illustrated after the arrival of the foliage pathogen, *Dothistroma septosporum*, in New Zealand in the early to mid-1960s. Over large areas of the country, *Pinus nigra* var. *laricio* and *P. ponderosa* went from growing very well by their natural-range standards to being unacceptably affected. This contributed strongly to a much-increased predominance of *P. radiata* even though it was itself considerably affected by the pathogen. The Forest Service, by growing large areas of species other than *P. radiata* in the first planting boom, during 1925 to 1935, was practising 'pre-emptive' species diversification (Burdon, 2001b). That turned out to be 'negative insurance', in that the slower growth of *P. nigra* and *P. ponderosa* were actually accompanied by greater disease susceptibility. While purely pre-emptive diversification today would be better informed, no assurance exists that it would be economically worthwhile.

There is a definite risk of a biotic crisis affecting *P. radiata* in New Zealand. The most likely form would be an extremely severe fungal disease. This is partly because of the profile of climatic hazards in which we grow *P. radiata*, which stem from growing a winter-rainfall species over large areas where summer rainfall is considerable, and partly because of the history of surprise appearance of pests. Any such crisis may well be accentuated by climatic change.

The likely worst case that is envisaged would be when commercially available genetic material of *P. radiata* would have inadequate resistance to the pest(s) concerned for restocking after harvest or for fresh afforestation. That would create an urgent need for

large-scale production of resistant planting stock if commercial forestry were to continue on the worse-affected sites. Such resistant stock would need to come from material intensively selected from within *P. radiata*, or *P. radiata* that is genetically engineered for resistance, or some hybrid(s) with other species, or even quite different species. Achieving that would be a challenge, even with good forward preparation, and could be impossible without such preparation.

While such a crisis may represent a low-probability contingency, it nonetheless constitutes a significant risk. This reflects the fact that risk level is the product of the probability of an adverse event and the seriousness of its consequences. The risk status here arises from the potentially dire consequences, especially if no proper advance preparations are made. Yet this sort of low probability is inherently very uncertain, making it difficult to construct a watertight business case for addressing the risk. Certainly, we can ill afford to go through acquiring an actuarial basis for such a risk.

Among the possible alternative forest plantation species, many grow very well in New Zealand. However, their roles, existing or potential, vary (Burdon and Miller, 1994). Some are complementary to *P. radiata* in their site tolerances ("extreme-site" species) and/or end-uses ("special-purpose" species). There are others ("contingency" species) which, while they may lack a current advantage for growing instead of *P. radiata*, could well become commercially competitive if, say, a new pest made it unattractive to grow *P. radiata*. These three categories are not mutually exclusive. For instance, Douglas-fir belongs in all three categories, having much better snow resistance than *P. radiata*, being better than it for structural timber, and being a contingency species for certain site categories. With Douglas-fir, the combination of site tolerances and its value as a timber species have led to active genetic improvement and management of genetic resources (Shelbourne et al., 2007). But, at the other end of the scale, there are serious concerns over the genetic conservation and management of species that are purely of contingency status, notably several Mexican and Central American pines. The existing plantings of those species in New Zealand typically represent population samples that are much less than ideal for conserving within-species genetic diversity. Moreover, they are often under severe threat of further attrition or even extirpation.

The Mexican and Central American pines have the great attraction of having very different spectra of disease resistance from *P. radiata*, reflecting their summer-rainfall habitats in contrast to the winter rainfall in the natural range of *P. radiata*. They are generally little, if at all, affected by several fungal diseases that can severely affect *P. radiata* in New Zealand, notably *Dothistroma* needle blight and *Diplodia*-associated shoot dieback. Moreover, they have proved much

more resistant than *P. radiata* to inoculation with the pitch canker fungus *Fusarium circinatum* (Hodge & Dvorak, 2000).

Some of the Mexican pines of interest are quite closely related to *P. radiata*, with a potential for hybridisation (Dungey et al., 2003). However, it is still very difficult, if possible at all, to cross these species with *P. radiata*, so much research remains to be done if crossing is to become readily achievable.

Unfortunately, the institutional and regulatory context of New Zealand's forestry sector, and some aspects of public policy, militate strongly against retaining appropriate genetic resources of many of the alternative species, for reasons I will now review.

Institutional aspect

Major and ongoing changes have occurred in the New Zealand forestry sector during the last 20 years. Outlined earlier by Burdon & Carson (1999), they have continued. The changes, occurring after the dissolution of the Forest Service in 1987, have involved: plantation forest ownership, corporate structures within the owners, management personnel therein, and associated business focus, along with elements of market failure. The consequences have been several-fold. Risk-management motivations among forest owners have changed, but more of that later. Perceptions of the economics of alternative management regimes have changed, partly through a lack of short-term market signals on the inherent worth of wood from older trees. One result has been a major lowering of harvest ages, which has created pressures to fell trees that would otherwise be left standing.

These developments have had serious implications for preservation of genetic material that could be of much long-term strategic significance. As indicated earlier, this genetic material includes genetic resources of *P. radiata* in the form of collections of native provenances that have contributed little if at all to our historical stocks, and spare material from the front-line breeding programme. It also includes plantings of other species which may serve as back-up for *P. radiata*, notably the contingency species. While there was provision for covenant protection of genetic material of likely significance, and plenty of covenants were imposed, the effectiveness of covenant protection is limited (Burdon & Carson, 1999). The changes in forest ownership, typically with even more rapid changes of thinly-spread management personnel, resulting confusion among those personnel, incentives for them to produce positive short-term cash flows, disincentives for them to 'rock the boat', and a general lowering of rotation ages, have all been conducive to accidental felling of genetic material. Yet the breeders who nominally control the covenanted material have been effectively beholden to the forest owners for their

funding. They are, therefore, naturally reluctant to try to block felling of material of unproven future value, or to seek reprisals for totally unauthorised felling. Indeed, Dr T. E. Richardson (Scion, personal communication, 2008) has been moved to say "The value of a covenant can sometimes rest in the usefulness of the paper on which it is written for wiping away the tears when the material gets felled."

An overarching issue, though, lies in the risk-management considerations for various forest owners. Several of the major players represent overseas interests for whom entire New Zealand operations can be but a small part of global risk spread. They, therefore, have limited motivation for proactive management of certain risks. This is especially true for low-probability events with potentially dire consequences, such as a biotic crisis for *P. radiata*. For various reasons, the management personnel may feel even less incentive to address such risks. Even among the 'small players' in our forestry sector, who account for a significant proportion (apparently ca 30%) of the plantation forest (MAF, 2007), many may have limited risk exposure to *P. radiata*, if their forestry investments form part of risk-spread portfolios. Thus, instead of the larger entity, namely the forestry sector, having greater risk spread than the individual players, we have the opposite, which might be termed 'inverse risk spread'. To state the situation in other terms (Prof. R. J. Bowden, Victoria University of Wellington, personal communication, 2008), the extreme predominance of *P. radiata* means that the "private risk" exposure is actually less than the "public risk" exposure which involves the national economy.

This situation for the forestry sector should not be considered in isolation. While this sector is large, contributing to 10% of national export receipts (MAF, 2007), the pastoral sector, together with its ancillary and processing industries is even larger, contributing ca 50% of New Zealand's export receipts (MAF, 2007). Yet the pastoral sector has a major exposure to the risk of an outbreak of foot and mouth disease in farm animals, with many overseas interests just waiting for a pretext to put up non-tariff trade barriers. This risk exposure, even if potential impacts are only short-term, much exacerbates the danger for New Zealand of lax or misguided risk management in the forestry sector.

Regulatory context

New Zealand has a strong system of border security based on plant and animal quarantine. This befits an island country that is still free of many dangerous pests, and is heavily dependent on primary-industry exports in a world where trade barriers may appear upon almost any pretext. This border security system represents a basic mechanism for implementing the Biosecurity Act of 1993, which superseded earlier

legislation. Other mechanisms include a system for response to incursions that will doubtless occur despite the best efforts of border control, which is now outlined in the Policy for the Ministry of Agriculture and Fisheries' Responses to Risk Organisms (MAF Biosecurity, 2008).

There is clearly a tension between the considerations of maintaining good border security, on the one hand, and acquiring germplasm that would be need to confer resistance to serious pests. Any importations of new germplasm will incur some risk, however small, yet genetic resistance may offer the only satisfactory long-term solution. Thus, any absolutist position is unsatisfactory. In the past, it was deemed that importing certain categories of plant material, such as conifer seeds, did not pose unacceptable risks. In fact, innumerable importations have occurred without importing serious pests. There have, however, been a few documented cases where such importations have brought in pests. For example, the leaf-spot fungus *Marssonina brunnea* Ellis & Everhart evidently gained entry on poplar seed (Spiers, 1989, 1998). The seed, however, represented relatively high-risk material imported in a crash programme to combat two other disease fungi (*Melampsora* spp.) for whose entry no advance preparations had been made. At this stage, two points could be made. First, our own border security was no defence against wind-borne *Melampsora* spores crossing the Tasman Sea (op. cit.). Second, it is unproven that various other serious forest-pest incursions have actually resulted from importing germplasm; certainly, it is most unlikely that this happened with the arrival of *Dothistroma* in New Zealand. Moreover, internal quarantine restrictions aimed at containing *Dothistroma* within the country proved futile, and yet significantly impeded the delivery of genetic gain from the *P. radiata* breeding programme (Burdon, 2001b).

Despite these considerations, the tide has definitely turned against the relatively permissive climate that we used to enjoy for importing germplasm. Forest pests themselves are becoming globalised, making it much more difficult to target areas from which importations can be readily approved. As a prime example, the arrival of the pitch canker fungus in California, and its spread to South Africa (Viljoen et al., 1997) and Chile (Wingfield et al., 2002), have greatly reduced the places from where *P. radiata* seed can be imported. This situation includes making the natural stands essentially unavailable as a source of fresh germplasm. Also, this pitch canker hazard now rules out further importations of pines from Mexico/Central America, which is the most promising source of disease resistant stock for New Zealand conditions. Admittedly, protocols now exist for importing tissue cultured material, which could even be screened for the asymptomatic presence of the pitch canker as a latent pathogen, and the protocols have regulatory

acceptance (C. L. Hargreaves, Scion, personal communication, 2009). The procedures, however, may not work readily for all species of interest and, even if they do work, are costly and impractical for importing the broadly based population samples that are appropriate.

Along with the suspected capability of the pitch canker fungus to behave for periods a strictly latent pathogen has come a realisation that many other fungi can be cryptically present in tree tissues. While many may be true endophytes (Ganley et al., 2004, Ganley & Newcombe, 2006) that are beneficial or at least harmless, not all may be harmless. This realisation is likely to accentuate any existing wariness towards making future importations of fresh germplasm.

In addition, there has been an important change in the regulatory framework, with the Hazardous Substances and New Organisms (HSNO) Act of 1996, which is administered by the Environmental Risk Management Authority (ERMA). Under this Act, importing a species that is not known to be present in New Zealand needs regulatory approval. The issues are distinct from those of biosecurity, which in this context involves pests that may be associated with imported plant material. For forest trees, the HSNO Act is likely to be concerned mainly with potential invasiveness. Even so, if tree species need to be imported for pest resistance to combat a biotic crisis, ERMA may face challenges in issuing approvals without involving undue expense and delays. The situation for approving species that have been in New Zealand but are not currently so remains to be clarified.

Between these considerations, there are now much greater regulatory barriers to measures that would make good any losses of potentially resistant germplasm. Yet several factors have increased risk of losses. I have already addressed institutional factors in terms of the pattern of forest ownership and the risk-management motivations for major classes of owners. However, there are also important gaps in public policy, which I will now address.

Public policy gaps

Two key instruments of public policy in New Zealand are seen as seriously deficient in addressing the need to provide for using genetic resistance to combat a biotic crisis arising from an uncontained incursion, or a *de novo* mutation, of a pest affecting *P. radiata*.

Representing an explicit policy statement is the Ministry of Agriculture and Forestry Forest Biosecurity Policy (MAF Biosecurity New Zealand, 2008), a seemingly comprehensive document which explicitly overrides preceding documents. The focus of that document is on border security, and the organisation of responses to contain and extirpate incursions of

pests that escape exclusion or interception by border security. However, no mention is made of conserving or managing germplasm that could provide the genetic resistance that might be needed to live comfortably with the pests that do escape. This evidently reflects a restricted brief, yet a submission made personally, in response to a call for submissions, has brought no evident revision of that brief.

The other policy instrument is less explicit but still important. It represents funding practice by the Foundation for Research, Science and Technology (FRST), in co-funding of research and genetic improvement. Specifically, this involves the genetic improvement of *P. radiata* and research on and improvement of alternative species ("Diverse Species"), in two different consortia involving Scion and industry parties. A heavy emphasis by FRST on responsiveness to industry wants is not a good mix with the divergence that exists between private and public risk in connection with the monoculture of *P. radiata*. It means limited commitment to addressing genetic resources of both *P. radiata* and purely contingency species. FRST have shown reluctance to be diverted from promoting "transformational" science and technology by addressing the potential for a biotic crisis in *P. radiata* after an uncontained pest incursion. Yet the application of transformational science and technology will depend totally on the biological security of the primary production base.

Steps needed

To maintain the germplasm in a form that can be used readily will require a number of measures. Some of the measures represent immediate practical steps. Others represent development of new technologies, some of them 'transformational' in themselves. While some of the measures are already being addressed, they will need greater commitment. Crucially, such commitment will need to come from a range of parties. Policy makers will need to recognise the problems and take a lead, in policy *per se* and in providing inducements for the sector as a whole. Parties funding research and development will need to support both immediate steps and the technology development. Finally, various growers will need to be committed because they inevitably host and manage the germplasm in a form that can be used.

Immediate practical steps include:

- renewal of gene-resource plantings of *P. radiata*;
- stocktaking of plantings of other species of contingency-species status, to help secure preservation and target seed collections; and
- acquiring better information on site tolerances,

management needs, and utilisation challenges of various contingency species.

Technology development needs to include:

- identification of genetic markers to quantify and identify pollen contamination of gene-resource plantings of *P. radiata*;
- Refinement of assays of seed or *in-vitro* cultures for improving safety of importation, in the light of how prevalent endophytes are now proving to be;
- much extended hybridisation technology, to introduce resistance genes from other species into *P. radiata*, involving a far less tentative approach;
- rapid-propagation technology, to supplement the meagre onshore seed sources available for various species of contingent interest, which will likely entail developing and refining *in-vitro* culture for those species; and
- discovery and characterisation of disease resistance genes, for targeted incorporation into *P. radiata* by either hybridisation or genetic engineering.

These technologies represent a portfolio, with potential redundancy. However, given risks of failure in developing both individual technologies and technology chains, potential redundancy needs to be accepted.

Concluding Remarks

Much emphasis has been placed on the situation in New Zealand, as a case history. While the issues addressed are writ particularly large here, with an associated focus on fungal diseases, they are likely to be shared significantly by a number of other countries, especially in an age of globalisation. For practical solutions, both broadly based commitment and the development of adequate new technology portfolios will be crucial.

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References

- Burdon, R. D. (2001a). *Pinus radiata*. In F. T. Last (Ed.), *Ecosystems of the World, Vol. 19, Tree Crop Ecosystems*, (pp. 99-161). Amsterdam, The Netherlands: Elsevier.
- Burdon, R. D. (2001b). Genetic aspects of risk – species diversification, genetic management and genetic engineering. *New Zealand Journal of Forestry*, 45(4), 20-25.
- Burdon, R. D., & Carson, M. J. (1999). Conservation and management of genetic resources of commercial forests in New Zealand: Challenges of institutional changes and new technology. In C. Mátyás (Ed.), *Forest Genetics and Sustainability*. Proceedings of IUFRO Conference, August 1998, Beijing (pp. 235-246). Dordrecht, The Netherlands: Kluwer.
- Burdon, R. D., & Gea, L. D. (2006). Pursuit of genetic gain and biotic risk management for *Pinus radiata* in New Zealand. In C. F. Mercer (Ed.), *Breeding for Success: Diversity in Action. Proceedings of 13th Australasian Plant Breeding Conference, April 2006, Christchurch, New Zealand*, (pp. 133-140) Retrieved in March 2009 from <www.apbc.org.nz>
- Burdon, R. D., & Miller, J. T. (1994). Alternative species revisited: Categorisation and issues for strategy and research. *New Zealand [Journal of] Forestry*, 40(2), 4-9.
- Burdon, R. D., Carson, M. J., & Shelbourne, C. J. A. (2008). Achievements in forest tree genetic improvement in Australia and New Zealand 10: *Pinus radiata* in New Zealand. *Australian Forestry*, 71(4), 263-280.
- Dick, M. A., Bulman, L. S., & Crane, P. E. (2006). *Nectria fuckeliana* infection of *Pinus radiata* in New Zealand: research approach and interim results. In J. C. Guyon (Comp.) *Proceedings of the 53rd Western International Forest Disease Work Conference, Jackson Hole, Wyoming. 26-30 September 2005*. Ogden, UT, USA: U.S. Department of Agriculture, Forest Service, Intermountain Region.
- Dungey, H. S., Carson, M. J., Low, C. B., & King, N. G. (2003). Potential and niches for inter-specific hybrids with *Pinus radiata* in New Zealand. *New Zealand Journal of Forestry Science*, 33, 295-318.
- Durán, A., Gryzenhout, M., Slippers, B., Ahumada, R., Rotella, A., Flores, F., Wingfield, B. D., & Wingfield, M. J. (2008). *Phytophthora*

- pinifolia* sp. nov. associated with a serious needle disease of *Pinus radiata* in Chile. *Plant Pathology*, 57(4), 717-727.
- Ganley, R. J., & Newcombe, G. (2006). Fungal endophytes in seeds and needles of *Pinus monticola*. *Mycological Research*, 110, 318-327.
- Ganley, R. J., Brunsfield, S. J., & Newcombe, G. (2004). A community of unknown, endophytic fungi in western white pine. *Proceedings of the National Academy of Sciences of the USA*, 101, 10107-10112.
- Hodge, G. R., & Dvorak, W. S. (2000). Differential responses of Central American and Mexican pine species and *Pinus radiata* to infection by pitch canker fungus. *New Forests*, 19, 241-158.
- Hunt, R. S. (2003). White pine blister rust. *Recent Developments in Mycology*, 1, 71-85.
- Liebhold, A. M., MacDonald, W. L., Bergdahl, D., & Mastro, V. C. (1995). Invasion by exotic forest pests: A threat to forest ecosystems. *Forest Science Monograph* 30.
- Ministry of Agriculture and Forestry (MAF). (2007). *International Trade Statistics*. Wellington, New Zealand: Retrieved from Ministry of Agriculture and Forestry. Retrieved in March 2009 from <<http://www.maf.govt.nz/statistics/index.htm>>
- Ministry of Agriculture and Forestry (MAF) Biosecurity New Zealand (2008). *Policy for MAF's Responses to Risk Organisms*. Wellington, New Zealand: Ministry of Agriculture and Fisheries.
- Schaberg, P. G., DeHayes, D. H., Hawley, G. J., & Nijensohn, S. E. (2008). Anthropogenic alterations of genetic diversity within tree populations: Implications for forest ecosystem resilience. *Forest Ecology and Management*. 256, 855-862.
- Shelbourne, C. J. A., Low, C. B., Gea, L. D., & Knowles, R. L. (2007). Achievements in forest tree genetic improvement in Australia and New Zealand 5: Genetic improvement of Douglas-fir in New Zealand. *Australian Forestry*, 70, 28-32.
- Smith, D. M. (2000). American chestnut, ill-fated monarch of the eastern hardwood forest. *Journal of Forestry*, 98(2), 12-15.
- Spiers, A. G. (1989). Introduction of poplar and willow pathogens into New Zealand and their effect. *New Zealand Journal of Forestry Science*, 19, 347-352.
- Spiers, A. G. (1998). *Melampsora and Marssonina* pathogens of poplars and willows in New Zealand. *European Journal of Forest Pathology*, 28, 235-240.
- Storer, A. J., Gordon, T. R., Wood, D. L., & Bonello, P. (1997). Pitch canker disease of pines: current and future impacts. *Journal of Forestry*, 95(12), 21-26.
- Viljoen, A., Wingfield, M. J., Marasas, W. F. O. & Coutinho, T. A. (1997). Pitch canker of pines – a contemporary review. *South African Journal of Science*, 93(9), 411-413 [Abstract retrieved in March 2009 from Google Scholar].
- Wingfield, M. J., Jacobs, A., Coutinho, T. A., Ahumada, R., & Wingfield, B. D. (2002). First report of pitch canker fungus, *Fusarium circinatum*, on pines in Chile. *Plant Pathology*, 51(3), 397 [Abstract retrieved in March 2009 from Google Scholar].