POTENTIAL AND NICHES FOR INTER-SPECIFIC HYBRIDS WITH PINUS RADIATA IN NEW ZEALAND

H. S. DUNGEY,

New Zealand Forest Research Institute,
Private Bag 3020, Rotorua, New Zealand

M. J. CARSON,

Carson Associates,
34 Parawai Rd, Ngongataha, New Zealand

C. B. LOW,

New Zealand Forest Research Institute,
Private Bag 3020, Rotorua, New Zealand

and N. G. KING

Cawthron Institute,
Private Bag 2, Nelson, New Zealand

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ABSTRACT

In New Zealand there are currently 1.59 million hectares of plantation *Pinus radiata* D.Don. Further expansion of the plantation resource in this country may have to occur outside the most suitable growing regions, while some existing plantation areas may undergo significant climatic changes. Therefore, species alternatives that have additional climatic and site tolerances need to be found. In addition, although *P. radiata* is fairly versatile, its intrinsic wood quality clearly limits product quality. Inter-specific hybrid combinations might provide a wider range of opportunities for wood quality improvement and disease resistance. This could be particularly important for biotic threats such as pitch canker (*Fusarium circinatum* Nirenberg & O'Donnell).

Some hybrids have already been produced and, even though these inter-specific crosses have shown lower viability and in some cases lower post-germination viability than intra-specific crosses, the benefits from introducing new attributes or increasing the range of attributes could still be worth pursuing. However, hybrids also have higher developmental costs in crossing and propagation such that greater complexity in breeding strategy may be required than with their pure-species counterparts. Therefore, pine hybrids in New Zealand need to be targeted to specific outcomes of high value. These priorities are most likely climatic (site- and climate-change related), biotic (extending the current plantation area into drought-, frost-, and snow-prone environments), and risk mitigation against the accidental introduction of biotic threats.

Keywords: hybrids; tree breeding; inter-specific hybrids; *Pinus radiata*.

INTRODUCTION

Pinus radiata has emerged as one of the most highly domesticated plantation forest species at the turn of the century (Burdon 2000). The species is relatively site-tolerant and has been planted widely, although over 90% of its current global resource is planted between latitudes 33.5ºS and 46.5ºS in Australia, Chile, and New Zealand (Lavery & Mead 1998) and within a relatively narrow climatic band dominated by winter rainfall (Grace *et al.* 1991). In New Zealand alone, there are currently 1.59 million ha of plantations of *P. radiata* (Ministry of Agriculture & Forestry 2002), representing a large proportion of the most productive land available for this species. Further expansions may occur as areas that are marginal for sheep farming are converted to forestry. However, limitations will also occur through the distance from the resource to the mill and to ports. Nevertheless, it is likely that most expansion would occur outside the most desirable growing regions. Therefore, *P. radiata* or *P. radiata* alternatives that are more tolerant to environments that are marginal for the current *P. radiata* resource need to be found in order to ensure the viability of expanding forests.

Producing new genotypes for new environments is possible through hybridisation with other species. In pines, some hybrids have been highly successful, particularly where the planting environment is outside the optimal range of the parent species. The hybrid between *Pinus elliottii* Engelm. and *P. caribaea* Morelet var. *hondurensis* Barrett & Golfari, planted on over 23 000 ha in Queensland, Australia, usually out-performs either pure species on wet sites and is considered equal to *P. caribaea* var. *hondurensis* on some of the better-drained sites (Dungey & Nikles 2000; Dieters *et al.* 1996; Powell & Nikles 1990). Where outright waterlogging is a problem, *P. elliottii* is the best performer (Lewty 1988). More recent results from 9- and 10-year-old data indicate that *P. caribaea* var. *hondurensis* can outperform the hybrid on some sites (J.Brawner pers. comm.). Nevertheless, it is the combined traits in the hybrid that perform more consistently than the same traits in either pure species across sites that is attractive. In particular, the hybrid has better straightness and wind-firmness than *P. caribaea* var. *hondurensis* (Dieters *et al.* 1996). In addition, managing a regime for one taxa is considerably simpler than managing multi-species regimes. *Pinus rigida* Mill. × *P. taeda* L. hybrids have been planted in Korea for over 30 years, consistently out-performing *P. rigida* (Hyun 1976; Byun *et al.* 1989). The success of these two examples of hybrids has contributed to the impetus for investigation into the potential of hybridisation with *P. radiata.*

In this paper we outline the potential for hybrids with *P. radiata* in New Zealand and the possible niches that they may occupy, starting with a brief explanation of the expectations for hybrids based on previous experience. Areas where hybrids may be useful for commercial forestry in New Zealand are discussed, and species that may be used for hybridisation with *P. radiata*. Early results of inter-specific crossing are presented.

PROS AND CONS OF HYBRIDISATION

Tree breeders are interested in hybrids because of the possibility of exploiting gain through heterosis. Heterosis, or hybrid vigour, is measured as the difference between the performance of the F_1 hybrid and the two parent species and has two common definitions — mid- and high-parent heterosis. Mid-parent heterosis is where the F_1 hybrid performs, on average, better than the value midway between the two parent species. High-parent heterosis is where the F_1 out-performs the best-performing parent species (*see also* Falconer & Mackay 1996; Verryn 2000; Dungey 2001). This definition holds where "performance" is any trait, but in tree breeding it usually refers to growth, wood properties, or disease resistance. In most reported examples of hybrid performance in tree species, hybrids are intermediate between parent species, and can show mid-parent heterosis (*see for example*, Dungey *et al.* 2000; Dungey 2001). High-parent heterosis is not common, but examples include volume and straightness in the hybrid between *P. elliottii* var. *elliottii* and *P. caribaea* var. *caribaea* (Nikles 2000), and volume in the *P. cembra* Thunb. × *P. monticola* D.Don cross (Blada 1994). Heterosis is also environment-dependent in many hybrids, and in the well-documented commercial hybrid of *P. elliottii* var. *elliottii* in Queensland, Australia, it is actually the complementarity of traits in the hybrid that give it an advantage over a range of sites compared with the pure species (Nikles 2000). Another classic case of complementarity is the *Eucalyptus urophylla* S.T.Blake × *E. grandis* Maiden hybrids in Congo (Vigneron & Bouvet 2000) and Brazil (Campinhos & Ikemori 1989). *Eucalyptus grandis* is faster growing, has better pulping properties, and is overall more productive than *E. urophylla*, but in these environments *E. grandis* is highly susceptible to canker. The hybrid is successful because of the growth traits contributed by *E. grandis* and the disease resistance conferred by *E. urophylla*. A final example where hybrids are used in certain environments is in South Africa, where the most common reason for breeding hybrid eucalypts is to extend forestry into areas that are economically marginal for the parent species (Verryn 2000).

Hybrids also have disadvantages. Hybrids can represent a genetic "dead-end" (Shelbourne 2000), as they are always one step removed from the improved parental populations. Hybrids are also not always successful and have biological barriers to production (*see for example*, Potts & Dungey 2004), but failures are not usually reported. The costs of hybrid programmes are greater because of their greater complexity, and vegetative propagation systems are required to capture any gain made. These disadvantages mean that hybrids must be targeted where their deployment will make real gains of economic importance, above those available from intra-specific selection and breeding.

LIMITATIONS FOR SUCCESSFUL PLANTATIONS OF *PINUS RADIATA* IN NEW ZEALAND

Biotic and Geographic Limitations

Apart from harvesting and processing costs, there are a number of factors that currently limit the distribution of the most productive *P. radiata* plantations in New Zealand. Geographic and climatic factors include steep terrain, soil type, wind exposure, and cold extremes, notably snow damage (Table 1) (Burdon 2000). At low temperatures, *P. radiata* can be susceptible to frost damage (–6ºC in summer, –14ºC in winter — Grace *et al.* 1991; Menzies & Chavasse 1982) and damage caused by the wet snow that falls particularly in Canterbury, Otago, and Southland is known to restrict siting of this species (Burdon & Miller 1992). High winds and heavy rain from tropical storms have caused toppling in large areas of North Island *P. radiata* plantation forests in the past, a recent example being Cyclone Bola in 1988, which damaged more than 30 000 ha (Grace *et al.* 1991). Climate change is likely to increase the frequency of such events in the future (Grace *et al.* 1991).

TABLE 1–Main factors involved in damage of *P. radiata* plantations in New Zealand. All of these agents reduce the value of the end crop by increasing the age of the rotation, reducing stocking, and/or reducing the form of the trees. Sources: Burdon & Miller (1992); Grace *et al.* (1991); Menzies & Chavasse (1982).

Factor	Common name	Problems caused
Abiotic factors		
Snow damage	–	Young trees (2–3 years old) suffer windthrow or wind breakage, older trees can have irreversible stem bending, often breakage. Lowers stocking and number of useful stems.
Wind damage	–	Damage to the leader, causing forking and bad form. Reduces value at rotation.
Wind throw	–	Breakage, leading to salvage harvesting with varying success.
Toppling	–	Young trees are pushed over, some recover, but have buttsweep and sinuosity
Socketing	–	Young trees in wet clay are blown around, loosening root grip, leaving a conical hole around the stem, often connected with toppling.
Frost damage	–	High mortality in the first 2 years. Lowers stocking, reducing value at rotation.
Drought	–	High mortality in the first 2 years. Lowers stocking.
Biotic factors (insects)		
Sirex noctilio	Wood wasp	Damages wood. Reasonable control obtained with parasitoids. Reduces value at rotation and can kill trees.
Hylastes ater	Black pine bark beetle	Ringbarking of stressed seedlings, particularly when planted on sites previously planted with *P. radiata*. Lowers stocking.
Biotic factors (fungi)		
Dothistroma pini	Needle blight	Needle loss. Slows growth and can contribute to dieback when severe. Can make trees more susceptible to Armillaria root rot. Increases rotation.
Sphaeropsis sapinea	Diplodia dieback	Leader dieback causing form problems. Infection of pruned stubs and other wounds. Slows height growth, stains wood, and can kill the tree in extreme cases. Reduces value at rotation.
Cyclaneusma minus	Needle cast	Needle yellowing and casting can be severe and causes considerable loss in growth.
Phytophthora cinnamomi	Phytophthora	Root rot slows growth and kills some trees in poor drainage (field and nursery).
Armillaria spp.	Root rot	Weakens root systems, lowers growth, and often causes toppling in conjunction with wind. Reduces stocking. Kills young plants.
Other biotic factors		
Trichosurus vulpecula	Brushtail possum	Breaks branches; eats young shoots, pollen cones, and young seed cones, strips bark from leaders, causing loss in growth and form and loss in seed-orchard yields. Can aid Diplodia dieback infection. Reduces value at rotation.

While the productivity of *P. radiata* plantations is currently not precluded by low rainfall, rainfall is likely to become limiting in the future due to climate change, particularly in areas such as the Canterbury Plains situated on the east coast of the South Island (Grace *et al.* 1991).

Biotic factors such as diseases and insect pests can also reduce or even destroy the economic returns on plantations (Table 1) (Lavery & Mead 1998). The disease that is presently the most important constraint for plantation growth is Dothistroma needle blight caused by *Dothistroma pini* Hulbary. As a direct response to this disease, a Dothistroma-resistant breed has been successfully developed for use in the warmer wetter areas, particularly in the central North Island where damage from this needle blight can be severe (Carson *et al.* 1991; Jayawickrama & Carson 2000). This breed is the only economically viable option for *P. radiata* plantations in these areas.

The potential threat to the *P. radiata* monoculture forest resource in New Zealand presented by pathogens and insects that are not yet found here could be disastrous. This means that in addition to the potential of hybrids for new planting environments being examined, hybrids that may be needed to replace the current resource should also be considered. There are a number of pests and pathogens whose introduction could threaten New Zealand's *P. radiata* plantations (Hosking *et al.* 1998). The potentially most important threats at the present time are pitch canker (*Fusarium circinatum*), Western gall rust (*Endocronartium harknessii* (J.P.Moore) Y.Hirats.), and the European pine shoot moth (*Rhyacionia buoliana* Denis & Schiffermüller). Of course, this list is by no means exhaustive; it represents those pests and diseases in a perceived "high-risk" category. There are many other overseas organisms that could also threaten New Zealand's forest resources if introduced (J.Bain pers. comm.).

Pinus radiata in California is highly susceptible to pitch canker and damage from this pathogen has caused severe losses in both natural stands and plantations elsewhere (Dvorak, Jordan, Hodge, & Romero 2000; Hodge & Dvorak 2000; Storer *et al.* 1997a, 2001). As a pathogen in exotic environments, pitch canker is spreading and so far has been reported in Haiti, Japan, Mexico, South Africa, and recently in Chile (Dwinell 1997; Wingfield *et al.* 2002). Pitch canker is dispersed in California through water splash and can be carried in air currents, but infection occurs only where wounds are present (Kuhlman *et al.* 1982; Dick 1998). Insects are therefore considered the primary agents of pitch canker transmission (Dick 1998). The fungus has also been isolated from seed from apparently healthy cones (Storer *et al.* 1997b). There is a real possibility that this fungus could become established in New Zealand, and it would most likely spread rapidly due to the presence of potential vectors and suitable climate (Dick 1998). However, while a possible vector for this pathogen is already present in New Zealand (*Hylastes* spp. beetles — Dick 1998), without the complete suite of vectors (as in California) the rate of spread and the severity would be difficult to predict.

Western gall rust has been recognised as a threat to New Zealand's *P. radiata* forests since the 1960s (Parmeter & Newhook 1967). Before the appearance of pitch canker, western gall rust was one of the major limiting factors to the perceived value of *P. radiata* in California (Parmeter & Newhook 1967). This rust causes severe damage through the formation of stem galls, resulting in death of young trees and stem deformation at later ages (Old 1981). The introduction of this disease would likely cause problems with new stand establishment, and in the longer-term reduce the health, vigour, and productivity of existing plantations (Old 1981). Perhaps the most important characteristic of this disease is that it has the potential to spread rapidly as it requires no alternate host and is wind dispersed (Hunt 1992) although the spores do not fly far (Peterson 1973). This disease is known to affect only the hard-pines, which includes all the species examined here (Old 1981).

The pine shoot moth *Rhyacionia buoliana* causes stem malformations and temporary loss of apical dominance (Burdon & Miller 1992; Ide & Lanfranco 1996), devaluing tree crops. In Chile, damage caused by this insect has severely affected plantations, particularly in the VIth and Xth regions (Ide & Lanfranco 1996; Toro & Gessel 1999). Although the climate in Chile is more Mediterranean than in the North Island of New Zealand where the majority of New Zealand's *P. radiata* is planted, if pitch canker, western gall rust, or the pine shoot moth arrive the effects could be severe. These effects would certainly be worsened because the current New Zealand plantation forestry resource is nearly 90% *P. radiata.* Inter-specific hybrids have the potential to provide some resistance to pests and diseases via the introduction of genes not currently known in the natural and cultivated population of *P. radiata*, but which are known to be present in some of the pines with which *P. radiata* can be crossed.

Product Quality Limitations

Increasing emphasis is being placed on wood quality forming an integral part of New Zealand *P. radiata* breeding objectives because of its economic importance (Jayawickrama & Carson 2000). Wood of highest value will be stiff, stable, and have good machinability and appearance qualities (Cown 1992; Burdon *et al.* 2001) and these properties are determined by a large number of interacting component traits (*see for example*, Kininmonth & Whitehouse 1991; Burdon & Low 1992; Cown 1992; Donaldson 1993; Donaldson & Burdon 1995). Unfortunately, *P. radiata* is less than ideal in a number of these areas, although various traits are currently being targeted. Among the known deficiencies of this species are the relatively low density and high spiral grain and microfibril angle of the corewood (generally equivalent to Rings 1 to 10 — Cown 1974, 1992). Improving corewood properties would improve the stiffness and stability of many sawn-timber products (Harris *et al.* 1976; Burdon *et al.* 2001). Although more needs to be known about the effect of site on these properties, inter-specific hybrids with other *Pinus* species might provide the opportunity for a step-wise improvement in some of these traits. Obviously, this can be so only where cross-compatible species have properties or a combination of properties that are superior or complementary to those of *P. radiata*.

KEY TARGET NICHES

There are a number of target niches where hybrids could help extend the range and productivity of plantations, while at the same time mitigating future climatic and biotic risks. These niches are all concerned with improving the economic return on current forestry or other land-use practices in these areas, or with mitigating economic losses from pests and diseases.

Higher-altitude sites where snow damage can be a major problem, particularly in the South Island and central North Island, are possible areas for expansion, although *Pseudotsuga* *menziesii* (Mirb.) Franco is currently being planted on such sites. New varieties of *Pinus radiata* with enhanced tolerance could be developed for areas of high Dothistroma risk, particularly for the central North Island, even though significant progress has already been made using intra-specific tree-to-tree variation (Carson *et al.* 1991). Recent climate change predictions indicate that the lower rainfall areas of Canterbury/Otago and the eastern North Island will become marginal for agriculture and should also be targeted (Grace *et al.* 1991). Pitch canker and western gall rust resistance should also be addressed as a form of biological insurance for the wider plantation resource of New Zealand.

INTRA-SPECIFIC VARIATION IN PINUS RADIATA

Because *P. radiata* is widely used, its natural habitat and origins have been well described (Lindsay 1932; Scott 1960; Forde 1966; Libby *et al.* 1968; Axelrod 1980, 1988; Eldridge 1983; Burdon 2000). In summary, *P. radiata* encompasses five distinct populations: Cedros Island, Guadalupe Island, and the mainland populations of Cambria, Monterey (Monterey Peninsula), and Año Nuevo (Burdon 2000). The Cambria, Monterey, and Año Nuevo populations on the Californian mainland are considered to make up the core of the natural occurrences of *P. radiata*, and are known as *P. radiata* var. *radiata*. The island populations of Cedros and Guadalupe are known as *P. radiata* var. *cedrosensis* (J.T.Howell) Silba and *P. radiata* var. *binata* (Engelm.) Lemmon respectively (Lavery & Mead 1998). All the natural populations of *P. radiata* are quite disjunct and have distinct characteristics (Burdon 2000; Lavery & Mead 1998).

The origin of the New Zealand land races is thought to be predominantly Año Nuevo and Monterey (Burdon & Miller 1992). The two island provenances, Cedros and Guadalupe, are therefore attracting attention as possible sources of genetic variation, as they are considered more drought-resistant, and have slightly higher wood density than the Californian mainland provenances, and Guadalupe appears to be straighter. The island provenances are also known to have greater resistance to western gall rust than the mainland provenances (Old *et al.* 1986; Kinloch *et al.* 1987). There has been quite a lot of work done on intra-specific hybrids of *P. radiata* in New Zealand (*see* Shelbourne 2000). Nevertheless, there is a limit to the range of the natural variation of *P. radiata* and increasingly breeders are considering incorporating variation from other pine species to enable targeting of some of the likely niches for future deployment (*see* Table 2).

POTENTIAL FOR IMPROVEMENT WITH INTER-SPECIFIC HYBRIDS — PREVIOUS EXPERIENCE AND FUTURE POSSIBILITIES

Interspecific hybrids with *P. radiata* may have the potential to quickly develop genotypes that more effectively target the niches outlined above. This is particularly so where the target environment occurs outside the natural variation and/or the ecological limits of this species (e.g., areas where *P. radiata* is susceptible to snow damage). Nevertheless, the potential for using hybridisation remains limited by crossability. This limitation is reflected in the phylogeny and systematics of these species, where there are a few general rules to follow. Firstly, hybrids between pines in different *Pinus* subsections generally will not produce viable seedlings (Little & Critchfield 1969; Price *et al.* 1998). Secondly, within subsections crossing some species may produce variable numbers of viable hybrid plants. *Pinus radiata* has recently been classified within the Subsection

TABLE 2–Likely target niches for inter-specific combinations that might be tested in New Zealand.

Target niche	Species combination	Sub-section
Higher-altitude sites / snow damage	× *P. attenuata*	Attenuatae
	× *P. muricata*	Attenuatae
Frost and cold damage	× *P. attenuata*	Attenuatae
	× *P. muricata*	Attenuatae
High Dothistroma risk	× *P. muricata*	Attenuatae
Lower rainfall	× *P. greggii*	Oocarpae
Pitch canker resistance	× *P. tecunumanii*	Oocarpae
	× *P. oocarpa*	Oocarpae
Improved wood properties	× *P. tecunumanii*	Oocarpae
	× *P. oocarpa*	Oocarpae
	× *P. pringlei*	Oocarpae

Attenuatae along with *P. attenuata* Lemmon and *P. muricata* D.Don (Price *et al.* 1998). These species represent the California closed-cone pines, and are not readily crossable with other taxa, including the group of Mexican pines (e.g., four species in Table 2), with which they were previously grouped as subsection Oocarpae by Little & Critchfield (1969).

Under the old classification by Little & Critchfield (1969), the pines now within Attenuatae (Price *et al.* 1998) were previously grouped with *P. greggii* Engelm. ex Parl., *P. oocarpa* Schiede ex Schltdl., *P. patula* Schltdl. & Cham., and *P. pringlei* Shaw in the Oocarpae. *Pinus tecunumanii* T.Eguiluz Piedra & J.P.Perry was described in the early 1980s (Eguiluz Piedra & Perry 1983), and was previously known as *P. patula* Schlechtend. & Cham. var. *tecunumanii* (Eguiluz & J.P.Perry) B.T.Styles (Price *et al.* 1998). A recent RAPD marker study by Dvorak, Jordan, Hodge, & Romero (2000) indicated that the Attenuatae group (in the classification by Price *et al.* 1998) is actually quite distinct from the rest of the Oocarpae. Crossing between these two groups is therefore likely to be more difficult than within the Attenuatae. However, as a basis for the production of hybrids, those species in Attenuatae (*P. muricata*, *P. attenuata*) and the majority of those in the old classification of Oocarpae by Little & Critchfield (1969) (i.e., *P. greggii, P. oocarpa, P. pringlei, P. tecunumanii*) will be considered as potential crossing partners for *P. radiata*. *Pinus patula*, also a member of the Oocarpae, was not considered as it would potentially contribute improved pulping characteristics (not a priority in New Zealand) and limited resistance traits (*see* Dvorak, Hodge, Kietzka, Malan, Osorio, & Stanger 2000; Hodge & Dvorak 2000). A synopsis of some of the important characteristics of both the Attenuatae and Oocarpae species relevant to hybridisation with *P. radiata* follows. Later, the performance of these species in New Zealand and some indications of their real potential are described. It is important to note that the species examined here are not the only options for crossing with *P. radiata*, but merely a list of useful species that will produce some progeny using control-pollination techniques.

Pinus attenuata

In most areas in New Zealand *P. attenuata,* or knobcone pine, has slower growth and larger variation in branching than *P. radiata* (J.T.Miller pers. comm., with reference to 12-

year-old trees at Naseby). Wood quality information for this species is lacking, but mean basic density in New Zealand of a sample of five trees aged 25–50 years was 410 kg/m^3 (Miller & Knowles 1988). In its natural range, *P. attenuata* experiences winter-dominant rainfall, which helps explain its high susceptibility to the pathogen *Dothistroma pini* in New Zealand (Miller & Knowles 1988). On most North Island sites, this species is so badly damaged that it is untenable (Miller & Knowles 1988). Pure *P. attenuata* does not grow as well as *P. radiata* even on South Island sites (compared at age 12 at Naseby) and plantations of the pure species are not considered an option (J.T.Miller pers. comm.). However, Miller & Knowles (1988) suggested that *P. attenuata* might have a role in hybridisation with *P. radiata* for drier or frosty sites in the South Island, where the risk of Dothistroma needle blight is minimal, and where the yield from *P. radiata* is marginal. This conclusion was based largely on limited testing (one F_1 hybrid seedlot and one F_3 hybrid seedlot) of *P. radiata* × *P. attenuata* hybrids incorporated into a New Zealand *P. attenuata* provenance trial. Progeny from crossing between four *P. attenuata* males and two *P. radiata* females were represented in plantings in 1978 at three South Island sites marginal for *P. radiata* (Miller & Knowles 1988). Compared with the pure-species controls, after 10 years the hybrids grew better, although their survival was lower. Further polycross tests were planted in 1998 and results from early growth and survival will soon be available. Qualitative observations of hybrids between *P. attenuata* and *P. radiata* planted in the northern Sierra Nevada in California showed that the hybrids were clearly superior in wet snow and survived wet snow events almost unscathed, while pure *P. radiata* was extensively damaged (R.D.Burdon pers. comm.). Hybrids with *P. attenuata* are therefore likely to survive better than pure *P. radiata* on New Zealand snow-prone sites.

In greenhouse tests on seedlings, *P. attenuata* appeared to be slightly more resistant to pitch canker than *P. radiata* but this species had a low resistance compared with some of the Mexican pines (Hodge & Dvorak 2000). The fungal pathogens *Cyclaneusma minus* (Butin) DiCosmo, Peredo & Minter, *Lophodermium* spp., and *Alternaria alternata* (Fries) Keissler have also been known to damage *P. attenuata* in New Zealand (Miller & Knowles 1988).

In summary, this species has the potential to contribute drought resistance, cold resistance, and resistance to damage from wet snow.

Pinus muricata

Pinus muricata is a potential candidate for hybridisation with *P. radiata* as some of the better plantations approach the productivity of *P. radiata* and wood properties of the two species are similar (Doran 1974; Shelbourne 1974; Schiedewind & Gammond 1980; Shelbourne *et al.* 1982; Wilkins & Bamber 1989). *Pinus muricata* also has some traits that are complementary to those of *P. radiata*: at an early age (1 year old) it is more resistant to damage by Dothistroma needle blight than is *P. radiata*, although it is still a winter-rainfall dominated species (Cobb & Libby 1968). However, this is possibly due to *P. muricata* obtaining its more-resistant adult foliage before *P. radiata*. Since the introduction of *D. pini* into Ecuador, *P. muricata* is being considered to replace *P. radiata* in areas of high risk, and to allow plantations at higher elevations (Millar 1985; Montenegro *et al.* 1997). Such a niche may be suitable for plantations of a *P. radiata* × *P. muricata* hybrid in

New Zealand. *Pinus muricata* has been observed to be less susceptible to western gall rust than *P. radiata* (46% *vs* 85%) and there is greater variation of infection rates among populations (*P. muricata* 9–100%, *P. radiata* 65–100%) (Kinloch *et al.* 1987). In greenhouse tests on a limited number of seedlings, *P. muricata* appeared to be marginally more resistant to pitch canker than *P. radiata* but had a lower resistance than some of the Mexican pines (Hodge & Dvorak 2000).

Pinus muricata is technically more challenging because of its more complicated biology. It is a variable species and, although highly oversimplified, is classified as having two distinct varieties found among the nine disjunct natural populations in California and Baja California (Critchfield 1967; Millar & Critchfield 1988). In northern California, this species has a distinct "blue" form, whereas in the populations south of Fort Ross, the provenances are known as "green muricata" (Millar & Critchfield 1988). The southern "green" and the northern "blue" provenances generally do not cross (Critchfield 1967; Millar & Critchfield 1988) and the northern "blue" provenances generally do not cross with *P. radiata*. Only the southern populations from the "green muricata", especially the populations of San Vicente and the Channel Islands, are sufficiently similar to *P. radiata* to be successfully hybridised. In studies by Critchfield (1966, 1967) which used small numbers of parent trees, the Sonoma provenance of *P. muricata* would not hybridise with *P. radiata* — despite certain striking similarities of bark, foliage, and (occasionally) cones between these two taxa.

Bannister (1966) indicated that the "blue" form of *P. muricata* was more desirable in New Zealand because of its greater frost resistance over winter and better form and branching than the "green" form. Although later provenance studies reported by Shelbourne *et al.* (1982) indicated that the majority of the faster-growing provenances were from the "green muricata" variant, he again recommended rejecting the southern provenances because of problems in tree form caused mainly by possum damage. From this study, the best two provenances were the Mendocino "blue" provenance and the Sonoma "green" population (Shelbourne *et al.* 1982). For improved hybrids, the Sonoma and Mendocino provenances would be the best place to start, even though the Sonoma provenance is difficult to cross.

In New Zealand, *P. muricata* from the Sonoma green provenance has been the fastest growing provenance at early ages, exceeding *P. radiata* controls on some cooler sites (at ages 5–6 years) (Shelbourne *et al.* 1982). At later ages, *P. muricata* out-performs *P. radiata* in growth only on the coolest sites (Shelbourne 1974). Wood density in *P. muricata* appears to be very similar to or lower than in *P. radiata* on most sites (from 360 kg/m^3 in the inner five rings, and up to 435 kg/m^3 for the five outermost rings, as discussed by Shelbourne 1974). The density-gradient from pith to bark appears to be lower in *P. muricata* than in *P. radiata* (Shelbourne 1974), an important contribution to a hybrid combination given that the gradient in *P. radiata* is relatively steep.

In summary, a hybrid with *P. muricata* would have potential for plantations in areas with high risk of Dothistroma needle blight and as biological insurance against an incursion of western gall rust. Apart from this, *P. muricata* is remarkably similar to *P. radiata*, something that may be an advantage for a hybrid between the two species, as it would be easily marketable under the same umbrella as *P. radiata*.

Pinus tecunumanii

Pinus tecunumanii occurs naturally in summer-dominant rainfall areas of tropical Central America, and is currently planted on a commercial scale in tropical and sub-tropical environments in Brazil, Colombia, and South Africa (Dvorak, Hodge, Gutiérre, Osorio, Malan & Stanger 2000). There are two important geographic sub-populations of *P. tecunumanii*: high altitude (approximately 1500–2900 m) and low altitude (approximately 450–1500 m) (Dvorak, Hodge, Gutiérre, Osorio, Malan & Stanger 2000). Provenances from the lower altitude group are resistant to drought. However, the species is not frost tolerant, suffers from top damage in high winds, and does not perform well in heavy clays (Dvorak, Hodge, Gutiérre, Osorio, Malan & Stanger 2000). In addition, this species is highly susceptible to fusiform rust (*Cronartium quercuum* f. sp. *fusiforme* (Berk.) Miyabe ex Shirai f.sp. (Hedgc. & N.Hunt) Burdsall & G.Snow), which is not yet present in New Zealand, and the bark beetle *Hylastes ater* (Paykull) in young seedlings. The fungal pathogen *Cylindrocladium* spp. also causes moderate damage. *Pinus tecunumanii* is susceptible to two different aphids — *Pineus laevis* (Maskell) (present in New Zealand) and *Cinara cronartii* Tissot & Pepper (not present in New Zealand).

The wood quality of *Pinus tecunumanii* appears to be good, although limited information is available. Dvorak, Hodge, Gutiérre, Osorio, Malan & Stanger (2000) stated that the wood has moderate to high density, and that density is more uniform within and between rings than that of *P. elliottii, P. patula*, and *P. taeda* in South Africa. The wood quality of this species in New Zealand is currently unknown. However, the main attraction to breeders of *P. radiata* is that *P. tecunumanii* has moderate to high tolerance to pitch canker (Dvorak, Hodge, Gutiérre, Osorio, Malan & Stanger 2000; Hodge & Dvorak 2000). In a greenhouse test of 9-month-old seedlings from 23 species, low-elevation *P. tecunumanii* was among the species with the least damage from this pathogen, although high-elevation *P. tecunumanii* had considerably lower survival and greater damage than the trees from low-elevation sources. In addition, *P. tecunumanii* is relatively resistant to Diplodia dieback (caused by *Sphaeropsis sapinea* (Fr.) Dyko & Sutton), a problem for *P. radiata* plantations in drier areas and summer-rainfall areas in New Zealand. In summary, *P. tecunumanii* might contribute pitch canker resistance and improved wood properties to a hybrid with *P. radiata* in New Zealand. However, this is a sub-tropical species and therefore any hybrids with this species might not be viable in the central North Island or the South Island and would have to be targeted at the warmer areas of the North Island.

Pinus oocarpa

The primary attraction of *P. oocarpa* in any New Zealand hybridisation programme with *P. radiata* is its resistance to pitch canker (Dvorak, Gutiérrez, Osorio, Hodge & Brawner 2000). This species was among the least damaged in a study of 9-month-old seedlings from a range of pines (Hodge & Dvorak 2000). *Pinus oocarpa* also has relatively high wood density (480 to 600 kg/m^3 in mature native stands) (Hess *et al.* 1950; Le Cacheux *et al.* 1959; Houkal *et al.* 1988, cited by Dvorak, Gutiérrez, Osorio, Hodge & Brawner 2000). In *ex situ* tests, the wood density from six provenances in Guatemala was between 450 and 520 kg/m^3 (55 trees of ages 35–51) (Dvorak 1981, cited by Dvorak, Gutiérrez, Osorio, Hodge & Brawner 2000). There is no information on the wood quality of this species under New Zealand conditions. One further advantage of *P. oocarpa* is that it is easily vegetatively propagated (Moura *et al.* 1998) and it is likely that the hybrid with *P. radiata* would be more easily propagated than pure *P. radiata*.

The disadvantages of *P. oocarpa* are that it is susceptible to wind throw, and susceptible to damage from the disease caused by *Cylindrocladium* spp. In colder climates, *P. oocarpa* is susceptible to frost damage — which is not surprising since it is a tropical to sub-tropical species from areas of summer rainfall (Dvorak, Gutiérrez, Osorio, Hodge & Brawner 2000). However, frost resistance is important for a large area of New Zealand and previous collections of the species that were planted in the central North Island have not survived (C.B.Low pers. comm.). *Pinus radiata* hybrids with this species would have to be restricted to warmer areas. In summary, *P. oocarpa* might contribute pitch canker resistance, improved wood properties, and enhanced propagation ability to a hybrid with *P. radiata* in New Zealand, targeted directly at the warmer areas of the North Island, particularly Northland.

Pinus greggii

Pinus greggii has a limited natural distribution in Mexico. This species occurs naturally in two distinct populations, one in the north (recently classified as *P. greggii* Engelm. ex Parl. var. *greggii*) and one in the south (*P. greggii* Engelm. ex Parl. var. *australis*) (Dvorak, Kietzka, Donahue, Hodge & Stanger 2000; Donahue & López-Upton 1996; Donahue *et al.* 1996). The northern population of *P. greggii* is more cold-tolerant than the southern populations, and the species as a whole is relatively drought-resistant (Dvorak, Kietzka, Donahue, Hodge & Stanger 2000). Density of juvenile and mature wood has been estimated as 458 and 515 kg/m^3 respectively, from natural stands of *P. greggii* var. *australis* (Murillo 1988, cited by Dvorak, Kietzka, Donahue, Hodge & Stanger 2000). This is slightly higher than the usual average tree basic density in New Zealand *P. radiata* of about 420 kg/m^3 (Burdon & Miller 1992), although the wood density of New Zealand plantation-grown *P. greggii* is not known. There is evidence to suggest that the density may be lower in an example from South Africa, where plantation-grown *P. greggii* was found to have a density of 373 kg/m^3 at 10 years of age (du Plooy & Venter 1981). Nevertheless, *P. greggii* var. *australis*, also from plantations in South Africa, had densities comparable to the natural stands at 453 and 508 kg/m^3 at only 6 years of age (Malan 1994).

Although *P. greggii* is resistant to *D. pini*, it is very susceptible to the woolly aphid *Pineus laevis*. In addition, although the northern population of *P. greggii* has some resistance to hail-induced Diplodia dieback (*Sphaeropsis sapinea*) in South Africa (Dvorak, Kietzka, Donahue, Hodge & Stanger 2000), the species has shown low resistance in off-site plantings in Brazil and South Africa. However, Diplodia dieback is unlikely to be a problem under New Zealand conditions. *Pinus greggii* is only marginally more resistant to pitch canker than *P. radiata* (Hodge & Dvorak 2000).

In New Zealand, 22 31-year-old *P. greggii* trees planted in Kaingaroa had an average diameter at breast height (dbh) of 346 mm, lower than the site mean for other Mexican pines in the same trial (T.G.Vincent pers. comm.; no *P. radiata* control comparisons were available). An additional problem for *P. greggii* is its susceptibility to possum damage (C.B.Low pers. comm.) as a result of which only 9% of the trees were acceptable in the final crop. This test was less than ideal for this species and is likely not to reflect the potential of the species on more suitable sites. However, *P. greggii* does not grow well on wet sites, perhaps an important factor in a country where water is limiting only in some of the colder sites. Unfortunately, this species also has a lengthy 33-month reproductive cycle, a disadvantage to any genetic improvement programme (Dvorak, Kietzka, Donahue, Hodge & Stanger 2000).

In summary, this species could contribute drought resistance, the chance of some improved wood properties, and improved resistance to *D. pini*.

Pinus pringlei

A *P. pringlei* hybrid would have an advantage over pure *P. radiata* in that *P. pringlei* has moderate-high resistance to pitch canker under glasshouse conditions (Hodge & Dvorak 2000) and high wood density (in natural populations, corewood averaged 604 kg/m^3, outerwood averaged 731 kg/m^3 (Murillo 1988, cited by Dvorak, Kikuti & Fier 2000); from South African 22-year-old plantations (unextracted) density was 490–730 kg/m^3, with an average of 530 kg/m^3 (Malan 1994)). Malan (1994) also found that solid-wood problems normally associated with spiral grain were low in this species. These properties mean that the wood of *P. pringlei* grown in South Africa and from native stands is excellent for solid-wood products (Dvorak, Kikuti & Fier 2000). This species is also moderately drought-tolerant and resistant to both Diplodia dieback and pitch canker (Dvorak, Kikuti & Fier 2000). Disadvantages include low frost tolerance, and an early grass stage where the seedling goes through a stage of no shoot development, indicating that greater management and weed control would be needed at early ages (Dvorak, Kikuti & Fier 2000). However, hybridising *P. pringlei* with *P. radiata* may be worth attempting. In summary, *P. pringlei* could contribute the following to a hybrid with *P. radiata*: improved wood characteristics, Diplodia dieback and drought tolerance, and resistance to pitch canker.

Tested Species

A number of the species outlined above have been tested as alternatives to *P. radiata* in New Zealand. These include *P. patula* (before the split from *P. tecunumanii* — P.Montgomery, M.J.Carson & G.D.Young unpubl. data), *P. pringlei*, *P. greggii* (T.G.Vincent, R.McConnochie, C.B.Low unpubl. data), and *P. oocarpa* (J.Miller unpubl. data; Montgomery, Carson & Young unpubl. data). Unfortunately, the majority of these species had poor survival or were badly malformed from severe possum damage. Survival of *P. pringlei* was very poor, but five surviving trees had average dbh of 348 mm (Vincent, McConnochie & Low unpubl. data). *Pinus greggii* had much better survival than *P. pringlei* and acceptable growth (average dbh of 334 mm on two sites at age 31) but was highly malformed and had the lowest proportion of acceptable stems of all the species tested (Vincent, McConnochie & Low unpubl. data). *Pinus oocarpa* was planted on a total of seven sites and so far no survivor from these plantings is known.

Although these results are discouraging, it must be remembered that the test material was unimproved and it is not these species that are targeted but the hybrids, and that hybrid performance is not always predictable from the performance of the individual parent species. A classic example of how different the performance of hybrids can be when compared with at least one of the parent species is seen in the hybrid between *Eucalyptus urophylla* and *E. grandis* planted widely in Congo (Vigneron 1995). In Congo, *E. urophylla* is relatively well adapted to the environmental conditions, while provenances of *E. grandis* are strongly maladapted (Baril *et al.* 1997). The *E. urophylla* × *E. grandis* hybrid is clearly superior, and it is the complementarity between traits from both parents that is contributing to this superiority.

TARGETING THE HYBRIDS

Inter-specific hybrid combinations should be targeted to specific niches of interest in New Zealand that are outside the current *P. radiata* growing areas and/or conditions (Table 2) (Burdon & Miller 1995). Of particular interest for the possibility of improving wood properties are the hybrids between *P. radiata* and *P. tecunumanii* (Table 2). These hybrids also offer prospects for protection of the forestry resource from pitch canker. The inter-specific hybrid combination of *P. radiata* with *P. pringlei* would have potential for improving solid-wood properties. However, *P. pringlei* is apparently not available in New Zealand in sufficiently high numbers to enable good tests to be undertaken. Other hybrid combinations will be most successful if they can be obtained from improved material. To ensure the best material is used, collaboration with international forestry organisations may be required.

Crossing Studies to Date

The earliest documented attempts by the New Zealand Forest Research Institute (NZFRI) to produce hybrids in the closed-cone pines included work (as yet unpublished) that resulted in a few trees putatively of the *P. radiata* × *P. muricata* hybrid. Although the hybrid origin of these trees was not conclusively proven, their habit appears intermediate between the parent species (C.B.Low pers. comm.). No crosses between *P. radiata* and the northern provenances of *P. muricata* produced any seed (Shelbourne 2000). The above crossing was followed by three periods of hybrid production — in 1976, in 1987–90, and during the mid- to late-1990s.

In 1974 artificial hybrids between *P. attenuata* and *P. radiata* were produced by NZFRI (Miller & Knowles 1988). Pollen had been collected from four *P. attenuata* trees in 1973, from parents derived from medium-high elevation (680–900 m) seed sources in mid-California. In 1974 this stored pollen was applied as a mix to two select clones of *P. radiata,* and the resulting hybrid seed was used to establish field trials.

The considerable promise shown in the trials established from the 1976 crosses between *P. attenuata* and *P. radiata* led to a further crossing. Polycrossing among 15 select parents of *P. radiata* and 15 selected ortets of *P. attenuata* (archived in 1987) (Table 3) was completed in 1994, and the resulting seed raised at the NZFRI nursery.

In 1988, NZFRI mixed irradiated *P. radiata* pollen (three treatments — 50,100, and 150 krad*) as “mentor pollen” (sterilised pollen used to facilitate fertilisation) with pollen of *P. greggii, P. patula,* and *P. muricata* in applications to conelets of *P. radiata*. A few seed were produced of all three putative hybrids, but there were no clear indications that pollen irradiation had influenced the limited success.

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* A standard measure of energy absorption where 1 rad = 0.01 joule/kg.

TABLE 3–Species and provenances selected and archived into clonal banks, for the 1987 pine hybrid project undertaken by Proseed in conjunction with NZFRI.

Species	Provenance	Rotations in New Zealand	No. clones archived	Ramets/clone
P. radiata	Guadalupe	1	50	7
P. radiata	Cedros	1	28	7
P. muricata	Sonoma	1	140	4
P. muricata	Mendocino	3	92	4
P. muricata	Trinidad head	1	15	4
P. attenuata	Siskiyou	1	15	8
P. greggii	Mexico	1	9	20
P. patula	Mexico	3	10	11

Other work on hybrids was initiated in 1987 by the seed-producing company Proseed. Through consultation with NZFRI, Proseed aimed to produce hybrids with increased tolerance to drought, poor soils, adverse climate, or disease. The ultimate aim was to continue crossing hybrids to incorporate a wide spectrum of genes for tolerance to these adverse influences. The species selected and archived in clone banks for this project are listed in Table 4. Selection of superior phenotypes and grafting operations were carried out between 1987 and 1990, cones and pollen were observed on many trees by 1993, and crossing operations were attempted in 1995 and 1997. In all trials, *P. radiata* was the pollen parent and, where possible, pollen mixes of at least six parents were used. In 1997 the crossing programme comprised only unsuccessful attempts to cross New Zealand Guadalupe and Cedros pollen with female parents of Mendocino and Sonoma provenances of *P. muricata.* Data on the putative hybrids from successful 1995 crosses are summarised in Table 4. To date, only the *P. attenuata* × *P. radiata* hybrid has been evaluated further.

TABLE 4–Successful crosses from 1987 pine hybrid project undertaken by Proseed in conjunction with NZFRI. (Note: these are crude seed yields and do not represent viable seed yields).

Female		Male		Cone and seed yields		
Species	Provenance	Species	Provenance	No. cones	No. seeds	Average seeds/ cone
P. radiata	Cedros	*P. attenuata*	Siskiyou	59	1364	23.1
P. radiata	Cedros	*P. greggii*	Mexico	21	23	0.91
P. radiata	Cedros	*P. muricata*	Mendocino	51	15	0.29
P. radiata	Cedros	*P. muricata*	Sonoma	75	16	0.21
P. radiata	Cedros	*P. patula*	Mexico	60	8	0.13
P. radiata	Guadalupe	*P. attenuata*	Siskiyou	6	67	11.2
P. radiata	Guadalupe	*P. greggii*	Mexico	15	0	0
P. radiata	Guadalupe	*P. muricata*	Mendocino	28	2	0.07
P. radiata	Guadalupe	*P. muricata*	Sonoma	42	0	0
P. radiata	Guadalupe	*P. patula*	Mexico	0	0	0

Further inter-specific crossing was initiated jointly in 1994 by NZFRI and the Queensland Forestry Research Institute (QFRI). This study aimed to combine the favourable growth rate of *P. radiata* in more temperate climates with favourable characteristics of *P. oocarpa* and *P. tecunumanii* — principally the pitch canker resistance of both sub-tropical species, possible wood quality improvement, and the enhanced ability of *P. oocarpa* cuttings to retain juvenility. Reciprocal crosses were carried out during 1996 and 1997, after an exchange of pollen between NZFRI (supplying QFRI with *P. radiata* pollen) and QFRI (supplying NZFRI with pollen of selected *P. oocarpa* and *P. tecunumanii)*. Single-pair crosses were made reciprocally between 16 genetically improved *P. radiata* parents and six pollen parents of *P. oocarpa* and 15 pollen parents of *P. tecunumanii*. Only nine seeds were produced from all *P. tecunumannii* or *P. oocarpa* × *P. radiata* crosses undertaken in north Queensland (M.J.Dieters pers. comm.). However, several hundred putative hybrid seeds have resulted from introducing pollen of these species on to *P. radiata* females (Table 5). Unfortunately the pollen viability was not as good as expected for these first crosses, which may explain to some extent the very low seed set attained. Some incompatibility was expected in crosses between these genetically distant species and the poor pollen germination would have been only one contributing factor. Further crossing between *P. radiata* and *P. tecunumannii* is planned at NZFRI to augment the seed already produced.

TABLE 5–Seed produced from inter-specific crossing between *P. radiata* and *P. oocarpa* or *P. tecunumanii* (a joint NZFRI-QFRI initiative). Note: the factorial between the males and females was not always complete.

Female		Male		Cone and seed yields		
Species	No. clones	Species	No. clones	No. cones	No. seeds	Average seeds/ cone
P. radiata	6	*P. oocarpa*	6	201	46	0.23
P. radiata	14	*P. tecunumanii*	15	455	365	0.80

Inter-specific Hybrid Trial Establishment

Only the *P. attenuata* × *P. radiata* hybrid has so far been tested in replicated field trials in New Zealand. The hybrids and controls arising from the 1976 crosses (*see* previous section) were planted in 1978 in small trials at Molesworth, Craigieburn, and Naseby — all frosty and/or snow-prone South Island sites. The Molesworth and Naseby sites were also subject to warm summers and low rainfall, although the Naseby site has since been abandoned (Miller & Knowles 1988). Survival of the hybrids had initially been adversely affected by severe *Botrytis* sp. infection in the nursery. By 1988, however, the hybrids had established a clear growth advantage over both the *P. radiata* and *P. muricata* controls (Miller & Knowles 1988).

The promise in those 1978 trials of the *P. attenuata* × *P. radiata* hybrid led to the polycrossing (details given earlier) and establishment of a further trial series. Additional material in the trial included seedlings of a single further hybrid-cross made in the United States (95/750 — *see* Table 6), plus control seedlots of the New Zealand landrace × the Guadalupe Island provenance of *P. radiata*, and an improved seed orchard seedlot (Table 6). A replicated trial with all seedlots was established on three dry South Island sites

TABLE 6–Seedlots in the *P. radiata* × *P. attenuata* hybrids trial planted in 1998 by NZFRI. Open-pollinated (OP) controls were included for both *P. radiata* and *P. attenuata.*

Seedlot	Female *P. attenuata* parent		*P. radiata* parent	
	No. parents	Provenances	No. parents	Provenances
P. attenuata × *P. radiata*	11	Siskiyou County, California.	16	Male parents from the New Zealand landrace and from the “268”, “850”, “875”, and “880” series in a pollen mix
	4	Josephine County, Oregon.	16	
P. attenuata-radiata ‘KMX’	Unknown	ex. Springs Farm, California.	Unknown	Unknown
P. radiata controls	–	–	15	OP controls using female parents from the “268”, “850”, “875”, and “880” series*
P. attenuata controls	11	OP controls from Siskiyou County†	–	–
	4	OP controls from Josephine County†	–	–

* Control *P. radiata* seedlots were collected from the same parents as those represented in the pollen used for the hybrid crossing.

† Control *P.attenuata* seedlots were collected from the same parents as those represented in the pollen used for the hybrid crossing.

in 1998 — Eyrewell Forest, Canterbury (low altitude), and Balmoral Station and Ribbonwood Station (high altitude). Surplus seedlings were established in a further smaller high-altitude trial at Mt Barker near Lake Coleridge (G.T.Stovold pers. comm.; N.J.Ledgard pers. comm.). These trials appear to be growing well, with the hybrids clearly out-performing both pure species at Balmoral Station and Ribbonwood, both of which are high-altitude sites with a continental climate (C.B.Low pers. comm.). The hybrids and pure *P. attenuata* also had a much higher survival rate than *P. radiata*. All sites have recently been assessed for early growth performance at approximately 4 years from planting.

Limited planting of the *P. attenuata* × *P. radiata* hybrid has occurred as control seedlots included in nation-wide provenance studies of *P. attenuata*. Results from one site (Naseby, tree age 15) have tended to confirm the slightly poorer growth of the hybrid on most of the warmer sites, plus its intermediate susceptibility to *D. pini* between the highly susceptible *P. attenuata* parent and the more resistant *P. radiata* (J.T.Miller pers. comm.). The newer trials described above will give a real indication of this hybrid's performance on the targeted cold dry sites in the South Island.

CONCLUSIONS

Appropriate hybrid combinations may provide the opportunity for rapid enhancement in traits of economic importance such as wood quality and pitch canker resistance for *P. radiata*. While the fertility of inter-specific crosses has been and will remain a major limiting factor for the utilisation of most inter-specific crosses (except with *P. attenuata*), the potential benefits are likely to warrant such programmes, particularly with the continued advances in vegetative multiplication. As shown here, the *P. attenuata* × *P. radiata* hybrid currently seems to have considerable potential for two main reasons. Firstly, early indications are that this hybrid is clearly superior at age 4 years on high-altitude sites in the South Island. Secondly, crossing with *P. attenuata* appears to be more successful than with some of the more distantly related pines. However, use of this hybrid in New Zealand will likely be confined to those cooler and drier sites which are less suitable for growth of the *P. radiata* parent species, and which are likely to remain free of disease caused by *D. pini.*

Whatever the success of hybrid progeny, it is difficult to deploy them commercially without either family forestry (using seedlings or vegetative propagules) or a clonal propagation system. The latter option includes a cycle for clonal testing, and clonal techniques have not been developed for the majority of the hybrid combinations mooted here for use in New Zealand. Even though nursery and propagation techniques are likely to be able to be adapted from current systems in *P. radiata*, some additional expense for development will be required. After the first generation, it may be possible to use open-pollinated F_2 seed orchards (e.g., *P. elliottii* × *P. caribaea* var. *hondurensis* outcrossed F_2 hybrid was used extensively in Queensland before systems for the mass propagation of F_1 were developed — Nikles 2000; D.G.Nikles pers. comm.). Nevertheless, to maximise the gains of outstanding hybrid genotypes, identification of superior clones and subsequent vegetative propagation will be the best option.

Higher developmental costs and more complex breeding strategies are required for hybrid trees than for their pure-species counterparts and they therefore need to be targeted to specific high-value or high-priority outcomes (see, for example, Dungey 2001). In New Zealand these priorities are most likely climatic and biotic: protection against introduction of pitch canker, the pine shoot moth, and western gall rust, and increasing the current plantation area into drought-, frost-, and snow-prone environments.

Finally, in this paper we have examined a number of potential hybridisation partners for *P. radiata.* The list presented here is far from comprehensive and there is no doubt that more species will present themselves in the future, particularly where new external pressures — climatic, biotic, or other — come into play. At this stage, crossability between species is limited. However, natural barriers to crossing may be overcome to some extent with new techniques such as *in vitro* fertilisation (Fernando *et al.* 1998), although genetic incompatibility will remain a constraint on the production of viable offspring. A further limitation to hybrid development in New Zealand is the tight restrictions placed by ERMA (Environmental Risk Management Authority) on species importation. If the species of interest is not present in this country, it is likely that the cost of quarantine and importation will prevent some species from being utilised.

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REFERENCES

AXELROD, D.I. 1980: History of maritime closed-cone pines, Alta and Baja California. *University of California Publications in Geological Sciences 120.* 143 p.

———1988: Paleoecology of a late Pleistocene Monterey pine at Laguna Niguel, Southern California. *Botanical Gazette 149*: 458–464.

BANNISTER, M.H. 1966: Notes on *Pinus muricata* and *Pinus attenuata*. *In* Weston, G. C. (compiler) "The Role of Pine Species Other than Radiata Pine in New Zealand Forestry". *Forest Research Institute, Rotorua, 22–24 March, FRI Symposium No. 7.* 3 p.

BARIL, C.P.; VERHAEGEN, D.; VIGNERON, P.; BOUVET, J.M.; KREMER, A. 1997: Structure of the specific combining ability between two species of *Eucalyptus*. II. A clustering approach and a multiplicative model. *Theoretical and Applied Genetics 94*: 804–809.

BLADA, I. 1994: Inter-specific hybridization of Swiss Stone Pine *Pinus cembra* L. *Silvae Genetica 43*: 14–20.

BURDON, R.D. 2000: *Pinus radiata*. Pp. 99–161 *in* Last, F.T. (Ed.) "Ecosystems of the World. Volume 19: Tree Crop Ecosystems". Elsevier, Amsterdam, The Netherlands.

BURDON, R.D.; LOW, C.B. 1992: Genetic survey of *Pinus radiata*. 6: Wood properties: variation, heritabilities, and interrelationships with other traits. *New Zealand Journal of Forestry Science 22(2/3)*: 228–245.

BURDON, R.D.; MILLER, J.T. 1995: Alternative species revisited: categorisation and issues for strategy and research. *New Zealand Forestry 40(2)*: 4–9.

———(Ed.) 1992: Introduced forest trees in New Zealand: Recognition, role and seed source. 12. Radiata pine (*Pinus radiata* D. Don). *New Zealand Forest Research Institute, FRI Bulletin No. 124/12*. 59 p.

BURDON, R.D.; BRITTON, A.J.; WALFORD, G.B. 2001: Wood stiffness and bending strength in relation to density in four native provenances of *Pinus radiata*. *New Zealand Journal of Forestry Science 31(1)*: 130–146.

BYUN, K.O.; KIM, Z.S.; SHIM, S.Y.; HONG, S.H.; SOHN, S.I. 1989: Review of Pitch-Loblolly hybrid pine (*Pinus rigida* × *P. taeda*) breeding researches in Korea and future strategy. *Research Report Forest Genetics Research Institute, Korea 25*: 204–211.

CAMPINHOS, E. Jr; IKEMORI, Y.K. 1989: Selection and management of the basic population *Eucalyptus grandis* and *E. urophylla* established at Aracruz for the long term breeding programme. Pp. 169–175 *in* Gibson, G.I.; Griffin, A.R.; Matheson A.C. (Ed.) "Breeding Tropical Trees: Population Structure and Genetic Improvement Strategies in Clonal and Seedling Forestry". Proceedings of IUFRO Conference, Pattaya, Thailand. Oxford Forestry Institute, Oxford, United Kingdom and Winrock International, Arlington, Virginia, USA.

CARSON, S.D.; DICK, A.M.P.; WEST, G.G. 1991: Benefits of the Dothistroma-resistant breed of radiata pine. Pp. 251–262 *in* Allen, J.C.; Whyte, A.G.D. (comp.) "New Directions in Forestry: Costs and Benefits of Change". Proceedings of Australia and New Zealand Institute of Forestry Conference.

COBB, F.W.; LIBBY, W.J. 1968: Susceptibility of Monterey, Guadalupe Island, Cedros Island and Bishop pines to *Scirrhia (Dothistroma) pini*, the cause of red band needle blight. *Phytopathology 58*: 88–90.

COWN, D.J. 1974: Wood density of radiata pine: its variation and manipulation. *New Zealand Journal of Forestry 19(1)*: 84–92.

———1992: Corewood (juvenile wood) in *Pinus radiata* – should we be concerned? *New Zealand Journal of Forestry Science 22(1)*: 87–95.

CRITCHFIELD, W.B. 1966: Crossability and relationships of the California big-cone pines. *USDA Forest Service, North Central Forest Experiment Station, St Paul, Research Paper NC-6*: 36–44.

———1967: Crossability and relationships of the closed-cone pines. *Silvae Genetica 16*: 89–97.

DICK, M. 1998: Pine pitch canker — the threat to New Zealand. *New Zealand Forestry 42(4)*: 30–34.

DIETERS, M.J.; MATHESON, A.C.; NIKLES, D.G.; HARWOOD, C.E. (Ed.) 1996: Proceedings of the QFRI-IUFRO Conference on "Tree Improvement for Sustainable Tropical Forestry". QFRI-IUFRO, Caloundra, Queensland. 536 p.

DONAHUE, J.K.; LÓPEZ-UPTON, J. 1996: Geographic variation in leaf, cone and seed morphology of *Pinus greggii* Engelm. *Forest Ecology and Management 82*: 145–157.

DONAHUE, J.K.; PERRY, J.P. Jr; SQUILLACE, A.E.; LIU, S. 1996: Geographic variation in stem-xylem terpene chemistry in native populations of *Pinus greggii* Engelm. *Forest Genetics 2(4)*: 217–225.

DONALDSON, L.A. 1993: Variation in microfibril angle among three genetic groups of *Pinus radiata* trees. *New Zealand Journal of Forestry Science 23*: 90–100.

DONALDSON, L.A.; BURDON, R.D. 1995: Clonal variation and repeatability of microfibril angle in *Pinus radiata*. *New Zealand Journal of Forestry Science 25(7)*: 164–174.

DORAN, J.C. 1974: Variations in growth of *Pinus muricata* provenances and comparison with *Pinus radiata*. *Australian Forestry Research 6(3)*: 19–24.

DUNGEY, H.S. 2001: Pine hybrids — a review of their use, performance and genetics. *Forest Ecology and Management 148*: 243–258.

DUNGEY, H.S.; NIKLES, D.G. 2000: An international survey of interspecific hybrids in forestry. Pp. 419–425 *in* Dungey, H.S.; Dieters, M.J.; Nikles, D.G. (comp.) "Hybrid Breeding and Genetics of Forest Trees". Proceedings of QFRI/CRC-SPF Symposium, Noosa, Queensland, Australia. Department of Primary Industries, Brisbane.

DU PLOOY, A.B.J.; VENTER, J.S.M. 1981: "The Kraft and Thermo-mechanical Pulp Quality of Ten-year-old *P. patula* and *P. greggii*". Council for the Scientific and Industrial Research, National Timber Research Institute, Pretoria, Republic of South Africa. 18 p.

DVORAK, W. S. 1981: Analyses of wood specific gravity on 55 trees of *Pinus oocarpa* Schiede in Guatemala. Internal document, CAMCORE Cooperative. College of Forest Resources, North Carolina State University. Raleigh, North Carolina, U.S.A. 7 p.

DVORAK, W.S.; KIKUTI, P.; FIER, I. 2000: *Pinus pringlei*. Pp. 174–187 *in* "Conservation and Testing of Tropical and Subtropical Forest Tree Species by the CAMCORE Cooperative", College of Natural Resources, NCSU, Raleigh, NC, USA.

DVORAK, W.S.; JORDAN, A.P.; HODGE, G.P.; ROMERO, J.L. 2000: Assessing evolutionary relationships of pines in the Oocarpae and Australes subsections using RAPD markers. *New Forests 20*: 163–192.

DVORAK, W.S.; GUTIÉRREZ, E.A.; OSORIO, L.F.; HODGE, G.R.; BRAWNER, J.T. 2000: *Pinus oocarpa*. Pp. 128–147 *in* "Conservation and Testing of Tropical and Subtropical Forest Tree Species by the CAMCORE Cooperative", College of Natural Resources, NCSU, Raleigh, NC, USA.

DVORAK, W.S.; KIETZKA, J.E.; DONAHUE, J.K.; HODGE, G.R.; STANGER, T.K. 2000: *Pinus greggii*. Pp. 53–72 *in* "Conservation and Testing of Tropical and Subtropical Forest Tree Species by the CAMCORE Cooperative", College of Natural Resources, NCSU, Raleigh, NC, USA.

DVORAK, W.S.; HODGE, G.R.; GUTIÉRREZ, E.A.; OSORIO, L.F.; MALAN, F.S.; STANGER, T.K. 2000: *Pinus tecunumanii*. Pp. 188–209 *in* "Conservation and Testing of Tropical and Subtropical Forest Tree Species by the CAMCORE Cooperative", College of Natural Resources, NCSU, Raleigh, NC, USA.

DVORAK, W.S.; HODGE, G.R.; KIETZKA, J.E.; MALAN, F.; OSORIO, L.F.; STANGER, T.K. 2000: *Pinus patula*. Pp. 148–173 *in* "Conservation and Testing of Tropical and Subtropical Forest Tree Species by the CAMCORE Cooperative". College of Natural Resources, NCSU, Raleigh, NC, USA.

DWINELL, L.D. 1997: Changing concepts in the pitch canker disease of pines. Pp. 227–234 *in* Proceedings of the IUFRO Working Party 7.02.02 on "Foliage Shoot and Stem Diseases of Forest Trees," 25–31 May, Quebec City, Quebec.

EGUILUZ PIEDRA, T.A.; PERRY, J.P. Jr 1983: *Pinus tecunumanii*: una especie nueva de Guatemala. [*Pinus tecunumanii*: a new species from Guatemala.] *Ciencia Forestal 7(41)*: 3–22.

ELDRIDGE, K.G. 1983: Genetic improvement from a radiata pine seed orchard. *New Zealand Journal of Forestry Science 12*: 404–411.

FALCONER, D.S.; MACKAY, T.F.C. 1996: "Introduction to Quantitative Genetics". 4th edition. Addison Wesley Longman Limited, UK. 464 p.

FERNANDO, D.D.; OWENS, J.N.; VON ADERKAS, P. 1998: In vitro fertilization from co-cultured pollen tubes and female gametophytes of Douglas fir (*Pseudotsuga menziesii*). *Theoretical and Applied Genetics 96*: 1057–1063.

FORDE, M.B. 1966: *Pinus radiata* in California. *New Zealand Journal of Forestry 11*: 20–42.

GRACE, J.C.; CARSON, M.J.; CARSON, S.D. 1991: Climate change-implications for *Pinus radiata* improvement. *New Zealand Journal of Forestry Science 21*: 123–134.

HARRIS, J.M.; JAMES, R.N.; COLLINS, M.J. 1976: Case for improving wood density in radiata pine. *New Zealand Journal of Forestry Science 5*: 347–354.

HESS, R.W.; WANGAARD, F.F.; DICKINSON, R.E. 1950: Properties and uses of tropical woods, II. *Yale University Press, School of Forestry, New Haven Connecticut, Tropical Woods 13(97)*. 132 p.

HODGE, G.R.; DVORAK, W.S. 2000: Differential responses of Central American and Mexican pine species and *Pinus radiata* to infection by the pitch canker fungus. *New Forests 19*: 241–258.

HOSKING, G.P.; CARSON, M.J.; DICK, M. 1998: Biosecurity strategies for the pitch canker threat to New Zealand's plantation forests. Pp. 6–10 *in* Devey, M.; Matheson, C.; Gordon, T. (Ed.) "Current and Potential Impacts of Pitch Canker in Radiata Pine". Proceedings of the IMPACT Monterey Workshop, Monterey, California, USA, 30 November to 3 December.

HOUKAL, D.; PONCE, E.; VILLALOBOS, D. 1988: Within-tree variation of wood specific gravity in ocote pine. *Turrialba 38(2)*: 97–104.

HUNT, R.S. 1992: Stem rusts of pine. *Canadian Forest Service, Pacific Forestry Research Centre, Forest Pest Leaflet No. 37*. 8 p.

HYUN, S.K. 1976: Inter-specific hybridization in pines with the special reference to *Pinus rigida* × *P. taeda*. *Silvae Genetica 25*: 188–191.

IDE, M.S.; LANFRANCO, D.L. 1996: Development of stem defects caused by *Rhyacionia buoliana* in Chile: an example in Region X. [Evolución de los defectos fustales producidos por *Rhyacionia buoliana* en Chile: un ejemplo en la Decima Region.] *Bosque 17(1)*: 15–19.

JAYAWICKRAMA, K.J.S.; CARSON, M.J. 2000: A breeding strategy for the New Zealand Radiata Pine Breeding Cooperative. *Silvae Genetica 49(2)*: 82–90.

KININMONTH, J.A.; WHITEHOUSE, L.J. (Ed.) 1991: "Properties and Uses of New Zealand Radiata Pine. Volume One — Wood Properties". New Zealand Ministry of Forestry, Forest Research Institute, Rotorua, New Zealand. 238 p.

KINLOCK, B.B.; LIBBY, W.J.; VOGLER, D.R. 1987: Variation in susceptibility to western gall rust in California closed-cone pines. Abstract. *In* Proceedings of the Western Forest Geneticist's Association Meeting, Prince George, British Columbia. http://plantbio.berkeley.edu/~bruns/papers/vogler1987b.html

KUHLMAN, E.G.; DIANIS, S.D.; SMITH, T.K. 1982: Epidemiology of pitch canker disease in a loblolly pine seed orchard in North Carolina. *Phytopathology 72*: 1212–1216.

LAVERY, P.B.; MEAD, D.J. 1998: *Pinus radiata*: a narrow endemic from North America takes on the world. Pp. 432–439 *in* Richardson, D.M. (Ed.) "Ecology and Biogeography of *Pinus*". University Press, Cambridge, United Kingdom. 527 p.

LE CACHEUX, P.M.; DE TUEDO, A; HUGHET, L. 1959: Project for the production of pulp and paper in Central America. *FAO Report, Vol. 1. No. FAO/CAIS/59/I*. 378 p.

LEWTY, M.J. 1988: Response to flooding of two *Pinus* species and their hybrid. Ph.D. thesis, University of Queensland, Australia.

LIBBY, W.J.; BANNISTER, M.H.; LINHART, Y.B. 1968: The pines of Cedros and Guadalupe Islands. *Journal of Forestry 66*: 846–853.

LINDSAY, A.D. 1932: Monterey pine (*Pinus radiata* D. Don) in its native habitat. *Canberra, Forestry and Timber Bureau Bulletin No. 10*. 57 p.

LITTLE, E.L.; CRITCHFIELD, W.B. 1969: Subdivisions of the genus *Pinus* (pines). *USDA Forest Service Miscellaneous Publication 1144*. 51 p.

MALAN, F.S. 1994: The wood properties and quality of *Pinus pringlei* Shaw and *P. greggii* Engel. compared with that of *P. patula* and *P. elliottii* grown in South Africa. *South African Forestry Journal 171*: 43–52.

MENZIES, M.I.; CHAVASSE, C.G.R. 1982: Establishment trials on frost-prone sites. *New Zealand Journal of Forestry 27(1)*: 33–49.

MILLAR, A. 1985: Ecuador (Short Note). *Commonwealth Forestry Review 64*: 194.

MILLAR, C.I.; CRITCHFIELD, W.B. 1988: Crossability and relationships of *Pinus muricata. Madroño 35*: 39–53.

MILLER, J.T.; KNOWLES, F.B. 1988: Introduced forest trees in New Zealand: Recognition, role and seed source. 5. *Pinus attenuata* Lemmon — knobcone pine. *New Zealand Ministry of Forestry, Forest Research Institute, FRI Bulletin No. 124/5*. 12 p.

MINISTRY OF AGRICULTURE & FORESTRY 2002: "1997 New Zealand Forestry Industry Facts and Figures 2001/2002". Ministry of Agriculture and Forestry, Te Manatu Ahuwhenua Ngaherehere, Wellington. 25 p.

MONTENEGRO, F.; MENESES, V.; WRIGHT, J.A. 1997: Growth of *Pinus muricata* provenances in the highlands of Ecuador. *Forest Ecology and Management 99*: 291–294.

MOURA, V.P.G.; DVORAK, W.S.; HODGE, G.R. 1998: Provenance and family variation of *Pinus oocarpa* grown in the Brazilian cerrado. *Forest Ecology and Management 109*: 315–322.

MURILLO, O. 1988: Natural variation in wood specific gravity of *P. greggii, P. leiophylla* and *P. pringlei*. *North Carolina State University, College of Forest Resources, Raleigh, CAMCORE Cooperative, CAMCORE Bulletin on Tropical Forestry No. 5*. 24 p.

NIKLES, D.G. 2000: Experience with some *Pinus* hybrids in Queensland, Australia. Pp. 14–26 *in* Dungey, H.S.; Dieters, M.J.; Nikles, D.G. (compilers) "Hybrid Breeding and Genetics of Forest Trees". Proceedings of QFRI/CRC-SPF Symposium, 9–14 April, Noosa, Queensland, Australia. Department of Primary Industries, Brisbane.

OLD, K.M. 1981: Western gall rust, a serious disease of *Pinus radiata* in California. *Australian Forestry 44*: 178–184.

PARMETER, J.R. Jr; NEWHOOK, F.J. 1967: New Zealand *Pinus radiata* is susceptible to western gall rust disease. *New Zealand Journal of Forestry 12*: 200–201.

PETERSON, R.S. 1973: Studies of *Cronatium* (Uredinales). *Report of the Tottori Mycological Institute (Japan) 10*: 203–223.

POTTS, B.M.; DUNGEY, H.S. 2004: Interspecific hybridization of *Eucalyptus*: key issues for breeders and geneticists. *New Forests 27*: 115–138.

POWELL, M.B.; NIKLES, D.G. 1990: Performance of Honduras Caribbean pine and its hybrid with slash pine in central south-east Queensland. *In* PEE×PCH F_1 seminar, Gympie.

PRICE, R.A.; LISTON, A.; STRAUSS, S.H. 1998: Phylogeny and systematics of *Pinus*. Pp. 49–68 *in* Richardson, D.M. (Ed.) "Ecology and Biogeography of *Pinus*". University Press, Cambridge, United Kingdom. 527 p.

SCHIEDEWIND, A.P.; GAMMOND, B. 1980: Strength and related properties of Bishop Pine 1. Strength of "blue race" Bishop Pine from three locations. *Wood Fibre 12*: 177–212.

SCOTT, C.W. 1960: "*Pinus radiata*". *FAO, Rome, FAO Forestry and Forest Products Studies No.14*. 328 p.

SHELBOURNE, C.J.A. 1974: Recent investigations of wood properties and growth performance in *Pinus muricata*. *New Zealand Journal of Forestry 19*: 13–45.

———2000: Some insights on hybrids in forest tree improvement. Pp. 53–62 *in* Dungey, H.S.; Dieters, M.J.; Nikles, D.G. (compilers) "Hybrid Breeding and Genetics of Forest Trees". Proceedings of QFRI/CRC-SPF Symposium, 9–14 April, Noosa, Queensland, Australia. Department of Primary Industries, Brisbane.

SHELBOURNE, C.J.A.; BANNISTER, M.H.; WILCOX, M.D. 1982: Early results of provenance studies on *Pinus muricata* in New Zealand. *New Zealand Journal of Forestry 27*: 50–66.

STORER, A.J.; GORDON, T.R.; WOOD, D.L.; BONELLO, P. 1997a: Pitch canker disease of pines: Current and future impacts. *Journal of Forestry 95*: 21–26.

———1997b: Current and future impacts of pitch canker disease of pines. *Journal of Forestry 10*: 21–26.

STORER, A.J.; WOOD, D.L.; GORDON, T.R.; LIBBY, W.J. 2001: Restoring native Monterey pine forests in the presence of an exotic pathogen. *Journal of Forestry 99(5)*: 14–18.

STYLES, B.T.; McCARTER, P.S. 1988: The botany, ecology, distribution and conservation of *Pinus patula* ssp. *tecunumanii* in the Republic of Honduras. *CEIBA 29*: 3–30.

TORRO, J.; GESSEL, S. 1999: Radiata pine plantations in Chile. *New Forests 18*: 33–44.

VAN DER KAMP, B.J.; TAIT, D.E.N. 1990: Variation in disease severity in the lodgepole pine-western gall rust pathosystem. *Phytopathology 80*: 1269–1277.

VERRYN, S.D. 2000: Eucalypt hybrid breeding in South Africa. Pp. 191–199 *in* Dungey, H.S.; Dieters, M.J.; Nikles, D.G. (compilers) “Hybrid Breeding and Genetics of Forest Trees”. Proceedings of QFRI/CRC-SPF Symposium, 9–14 April, Noosa, Queensland, Australia. Department of Primary Industries, Brisbane.

VIGNERON, P. 1995: Production and improvement of *Eucalyptus* varietal hybrids in the Congo. Pp. 259–273 *in* Traitements statistiques des essais de selection: strategies d’amélioration des plantes perennes. Actes du seminaire de biométrie et génétique quantitative. Montpellier, France. CIRAD, Montpellier, France.

VIGNERON, P.; BOUVET, J. 2000: Eucalypt hybrid breeding in Congo. Pp. 14–26 *in* Dungey, H.S.; Dieters, M.J.; Nikles, D.G. (compilers) “Hybrid Breeding and Genetics of Forest Trees.” Proceedings of QFRI/CRC-SPF Symposium, 9–14 April, Noosa, Queensland, Australia. Department of Primary Industries, Brisbane.

WILKINS, A.P.; BAMBER, R.K. 1989: Comparison of some wood properties of *Pinus muricata* and *Pinus radiata*. *New Zealand Journal of Forestry Science 52*: 20–22.

WINGFIELD, M.J.; JACOBS, A.; COUTINHO, T.A.; AHUMADA, R.; WINGFIELD, B.D. 2002: First report of the pitch canker fungus *Fusarium circinatum* on pines in Chile. *Plant Pathology 51*: 397.