PROSPECTS AND RISKS OF BIOLOGICAL CONTROL OF WILDING *PINUS CONTORTA* IN NEW ZEALAND

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ABSTRACT

Wildings from exotic tree plantations are a major threat to New Zealand's native vegetation and landscapes. The insects associated with the reproductive structures of the most significant invasive tree, *Pinus contorta*, are reviewed with regard to their suitability for biological control. Based on host species and structure specificity and their impact on seed production, *Conophthorus ponderosae* (Scolytidae), *Eucosma rescissoriana* (Tortricidae) and *Pissodes validirostris* (Curculionidae) are the most promising biocontrol candidates among the 16 North American or Eurasian insect species recorded as feeding on *P. contorta* cones. Further studies are needed to assess whether these insects could significantly reduce the rate of spread of *P. contorta* and would not pose a threat to any native plants or plantation forestry trees.

Keywords: invasive trees, biological control, weeds, *Pinus contorta*, cone and seed insects.

INTRODUCTION

For over a century, New Zealand forestry has favoured planting exotic trees over natives. Pines and other fast-growing conifers were used primarily and these currently cover about 20% of the total forested area (Purey-Cust and Hammond 1995). While this had the benefit of creating a highly successful forest industry, the spread of trees from exotic forests ("wildings") was soon recognised as a threat to conservation values and landscape character (Benecke 1967; Hunter and Douglas 1984). Similar problems with invasions of exotic trees exist in many other countries (e.g. Richardson and Higgins 1998).

The area of New Zealand currently affected by at least one wilding/ha is estimated at around 150,000 ha (Ledgard 1998). Conifers, which are often pioneering species in their native range, are the predominant invaders, notably *Pinus contorta* Dougl. ex Loud., *P. nigra* Arnold, and other pines, as well as *Larix decidua* Mill. and *Pseudotsuga menziesii* (Mirb.) Franco (Hunter and Douglas 1984; Ledgard 1988; 1998). Broadleaved trees such as *Acer pseudoplatanus* L., *Eucalyptus* spp., and *Acacia* spp. are also encountered (New 1984; Ledgard 1988). Invasions are most common in high country rangelands with little grazing pressure. However, the shade-tolerant *Ps. menziesii* and *Acacia* spp. also invade native forest. Although *Pinus radiata* D. Don. is by far the most commonly planted species, its importance as an invader is limited. Overall, *P. contorta* is the most aggressively spreading and most significant invasive tree species and has even been declared a noxious weed in the central North Island (Ledgard 1998). Trees aged only 5-8 years can produce cones and the comparatively light seeds can spread downwind for several kilometres (Ledgard 1998).

The spread of exotic trees is unwanted because it affects the value of unmanaged rangeland pasture and alters the landscape character (Hunter and Douglas 1984). It is particularly critical where native vegetation is invaded and possibly displaced (Hunter and Douglas 1984). The establishment of wildings is prevented on land intensively grazed by sheep. Otherwise, the spread of wildings can be reduced by removing the

trees that are seed sources and by various management practices (Ledgard 1998). Existing wildings can be controlled by manual removal, herbicide application or burning, but these methods are either labour intensive, expensive or may have undesirable side effects (Graeme 1997; Ledgard 1998).

Biological control of introduced weeds is often highly effective and generally regarded as ecologically viable (Waage and Greathead 1988; McFadyen 1998). The introduction of biocontrol agents to manage invasive tree species has been suggested for New Zealand and overseas (Kay 1994; Richardson and Higgins 1998). However, there has been no further action, probably because of the apparent conflict that biocontrol introductions might become forestry pests. Here, we review and examine the insects associated with *P. contorta* with regard to their suitability for biological control of this tree in New Zealand. Our focus is on inflorescence-feeding insects, i.e. 'cone insects', because they directly affect the production of seed and thereby potentially reduce the reproductive potential and the rate of spread of wildings. At the same time, such insects have only indirect effects on wood production and, consequently, less pest potential. However, there are still several potential conflicts of interest ranging from concerns about attack of non-target species to implications for future harvesting of self-established *P. contorta* stands. We begin with a review of the origin of *P. contorta* planted in New Zealand to assess implications of geographical variation of both the tree species and its associated cone insects.

ORIGIN OF *PINUS CONTORTA*

Pinus contorta, or lodgepole pine, is native to western North America and has been introduced to several other continents. In its native range, this pine has a remarkable ecoclimatic tolerance and distribution; it occurs from sea level to altitudes of almost 4000 m and from northern Mexico to the Canadian Yukon Territory (Wheeler and Critchfield 1985). Four subspecies of *P. contorta* are recognised, the coastal ssp. *contorta*, known as 'shore pine', the closely related ssp. *bolanderi*, the Cascade/Sierra Nevada ssp. *murrayana*, and the Rocky Mountain/Intermountain ssp. *latifolia* (Wheeler and Critchfield 1985). The history of *P. contorta* in New Zealand was reviewed by Miller and Ecroyd (1987). The first trees were planted in the 1880s from small seedlots of unknown origin. Most of the larger-scale plantations of this century originated from coastal Washington provenances of *P. contorta contorta* and from British Columbia provenances intermediate between ssp. *contorta* and ssp. *latifolia*. Because of its hardness, *P. contorta* ssp. *contorta* was also extensively used for erosion control in mountain ranges. All subspecies are present in New Zealand but the ssp. *contorta* is of greatest concern because it is the one spreading most rapidly (Ledgard 1998).

PROSPECTS FOR BIOLOGICAL CONTROL

The criteria important for the selection of a biocontrol agent have been discussed intensively (e.g., Cock 1986; Harley and Forno 1992; McFadyen 1998). Of particular importance for an introduction against *P. contorta* in New Zealand are: (i) narrow host range which should not include native plants or economically important tree species such as *P. radiata*; (ii) compatibility with the host ecotype and the climate in the target region; (iii) significant effect on seed production to achieve a sufficient reduction of spread and population of wildings; (iv) capability to disperse to scattered, remote infestations. This can be especially important where individual outlier trees are involved in initial spread.

The group of cone insects associated with *P. contorta* is diverse and species rich. In its native range, at least 14 species representing four orders have been found to attack seed cones (Table 1), and an additional species, the sawfly *Xyela alberta* (Curran) (Hymenoptera: Xyelidae), feeds exclusively on pollen cones (Hedlin *et al.* 1980). Furthermore, the pine cone weevil *Pissodes validirostris* attacks *P. contorta* planted in Europe (Table 1). Among these, all species of Coleoptera, Diptera and Hemiptera feed exclusively on cones, but several Lepidoptera also attack leaves, twigs or stems. Based on field observations, most species are restricted to pines but about one third have a host range that includes other conifers as well (Table 1). The insects specific to cones of

TABLE 1: Host specificity, distribution and impact of insects attacking *Pinus contorta* seed cones.

Taxa	Natural host range in addition to <i>P. contorta</i>	Host structure infested	Distribution	Impact*	References
COLEOPTERA					
<i>Conophthorus ponderosae</i> (Hopkins)	<i>Pinus flexilis</i> , <i>P. hartwegii</i> , <i>P. jeffreyi</i> , <i>P. lambertiana</i> , <i>P. leiophylla</i> , <i>P. monticola</i> , <i>P. ponderosa</i>	2nd-yr seed cones	W Canada, W USA, Mexico	L-S	Ruckes 1963 Hedlin <i>et al.</i> 1980 Miller and Ruth 1989 de Groot <i>et al.</i> 1994
<i>Ernobius nigrans</i> Fall	? <i>Picea mariana</i>	mature or dead seed cones	W Canada, W USA	L	Keen 1958 Hedlin <i>et al.</i> 1980 de Groot <i>et al.</i> 1994
<i>Paratimica conicola</i> Fisher	<i>Pinus attenuata</i>	mature or old seed cones	W USA	L	Keen 1958
<i>Pissodes validirostris</i> (Sahlberg)	<i>Pinus halepensis</i> , <i>P. nigra</i> , <i>P. pinaster</i> , <i>P. pinea</i> , <i>P. sylvestris</i> , <i>P. uncinata</i>	2nd-yr seed cones	Eurasia		Annala 1975 Alain Roques, pers. comm.
DIPTERA					
<i>Asynapta hopkinsi</i> Felt	several spp. of <i>Pinus</i> , <i>Abies</i> , possibly <i>Picea</i> and <i>Tsuga</i>	2nd-yr seed cones	Canada, W/E USA, N Mexico	L	Keen 1958 Hedlin <i>et al.</i> 1980 de Groot <i>et al.</i> 1994
HEMIPTERA					
<i>Leptoglossus occidentalis</i> Heidemann	<i>Pinus attenuata</i> , <i>P. jeffreyi</i> , <i>P. monticola</i> , <i>P. ponderosa</i> , <i>P. radiata</i> , several spp. of <i>Abies</i> , <i>Pseudotsuga</i> , <i>Tsuga</i>	pollen cones and seeds	W Canada, W USA	L	Hedlin <i>et al.</i> 1980 de Groot <i>et al.</i> 1994 Blatt and Borden 1996
LEPIDOPTERA					
<i>Choristoneura lambertiana</i> subretiana Obraztsov	<i>Pinus ponderosa</i>	seed/pollen cones, leaves and buds	W USA	S	Stark and Borden 1965 Hedlin <i>et al.</i> 1980

Table 1 continued over

Table 1 continued

Taxa	Natural host range in addition to <i>P. contorta</i>	Host structure infested	Distribution	Impact*	References
<i>Choristoneura pinus pinus</i> Freeman	<i>Pinus banksiana</i> , <i>P. ponderosa</i>	seed/pollen cones, buds and leaves	E/Central Canada/USA	?	Hedlin <i>et al.</i> 1980 de Groot <i>et al.</i> 1994
<i>Cydia toreuta</i> (Grote)	<i>Pinus banksiana</i> , <i>P. echinata</i> , <i>P. resinosa</i> , <i>P. taeda</i> , <i>P. virginiana</i> ?	2nd-yr seed cones	E Canada, E USA	L	Hedlin <i>et al.</i> 1980 de Groot <i>et al.</i> 1994
<i>Cydia</i> sp.				L	(Keen 1958)
<i>Dioryctria abietivorella</i> (Grote)	many spp. of <i>Pinus</i> , <i>Abies</i> , <i>Larix</i> , <i>Picea</i> , <i>Pseudotsuga</i> , <i>Tsuga</i>	2nd-yr seed cones, twigs and young tree stems	W USA Canada, W/E USA, N Mexico	L-S	Hedlin <i>et al.</i> 1980 (Miller and Ruth 1989) de Groot <i>et al.</i> 1994
<i>Dioryctria cambicola</i> (Dyar)	<i>Pinus coulteri</i> , <i>P. resinosa</i> , <i>P. ponderosa</i>	branches, twigs, buds, 2nd-yr seed cones	Canada, W USA	?	Lyons 1957 (Miller and Ruth 1989) de Groot <i>et al.</i> 1994
<i>Dioryctria reniculelloides</i> Mut. and Mun.	<i>Pinus banksiana</i> (?), several spp. of <i>Abies</i> , <i>Larix</i> , <i>Picea</i> , <i>Pseudotsuga</i> , <i>Tsuga</i>	seed/pollen cones, leaves and buds	Canada, W/E USA, N Mexico	L	Hedlin <i>et al.</i> 1980 (Miller and Ruth 1989) de Groot <i>et al.</i> 1994
<i>Eucosma rescissoriana</i> Heinrich	<i>Pinus monticola</i> , <i>P. albicaulis</i> several spp. of <i>Abies</i>	2nd-yr seed cones	W Canada, W USA	L-S	Hedlin <i>et al.</i> 1980 Miller and Ruth 1989 de Groot <i>et al.</i> 1994
<i>Holcocerina immaculella</i> (McDunnough)	<i>Pinus banksiana</i> , <i>P. resinosa</i> , <i>Pseudotsuga menziesii</i> , <i>Picea</i> <i>mariana</i> , <i>Larix laricina</i>	pollen cones, bud scales, (seed cones)	W/E Canada, W/E USA	L	Hedlin <i>et al.</i> 1980 de Groot <i>et al.</i> 1994
<i>Rhyacionia buoliana</i> (Schiff.)	<i>Pinus sylvestris</i> , <i>P. resinosa</i> , <i>P. radiata</i> , many other <i>Pinus</i> spp.	leaves, buds, shoots, seed cones	Eurasia, North/South America	?	Hedlin <i>et al.</i> 1980

* Direct impact on seed production categorised as low (L), severe (S) or unknown (?)

pinus (*Conophthorus ponderosae*, *Ernobius nigrans*, *Paratimbia conicola*, *Pissodes validirostris* and *Cydia toreuta*) would be unlikely to attack any plants native to New Zealand. Attack of *P. radiata* cones, which would interfere with seed production of this major forestry species, appears unlikely according to the host association in their native range. Although *Co. ponderosae* can be reared from eggs transferred to *P. radiata* cones in the laboratory (Ruckes 1963), an attack under natural conditions has never been reported. However, *Co. ponderosae* and *Pissodes validirostris* would attack cones of *P. ponderosa* and *P. nigra*, respectively, which have minor importance in plantation forestry. Although the host range on North American pines of the Palaearctic *Pissodes validirostris* is not well known, *P. radiata* planted in Europe are apparently not attacked (A. Roques, pers. comm.). *Eucosma rescissoriana* is another species with an apparently narrow host range; it attacks cones of *P. contorta* and *P. monticola*, which seem to be its main hosts, but also those of several *Abies* spp. (Hedlin *et al.* 1980) which are not significant forestry species. *Choristoneura* spp., *Dioryctria cambicola* and *Rhyacionia buoliana* have a host range limited to pines but they attack other host structures in addition to cones and have significant pest potential.

Many of these insects are associated naturally with only certain varieties of *P. contorta*. For example, *Cydia toreuta* does not occur anywhere near the coastal Pacific region and probably attacks only the ssp. *latifolia* (Hedlin *et al.* 1980). Similarly, *Ch. lambertiana subretiana* is apparently restricted to *P. contorta murrayana* (Hedlin *et al.* 1980). It is therefore critical to determine the exact variety and ecotype of wilding *P. contorta* to be able to match potential biocontrol agents. Similarly, agents should preferably originate from an area with a climate similar to that of the target region to increase the likelihood of establishment.

Several studies concluded that, overall, seed cones of *P. contorta* are seldom heavily attacked by insects in its native range (Keen 1958; Hedlin *et al.* 1980; Miller and Ruth 1989). However, high infestation rates of *P. contorta* cones occurred at several sites in coastal British Columbia involving *Co. ponderosae*, *Dioryctria* spp. and *E. rescissoriana* (Miller and Ruth 1989). In California, up to 90% of seed cones were infested by *Ch. lambertiana subretiana* (Stark and Borden 1965). Furthermore, *P. contorta* is apparently heavily attacked in Europe by the Palaearctic *Pissodes validirostris* (Annala 1975).

Thus, in view of these aspects, *Co. ponderosae*, *Pissodes validirostris* and *E. rescissoriana* appear to be the most suitable species to consider for biocontrol of wilding *P. contorta*. These species can cause significant damage to seed cones, they seem to be sufficiently host-specific and would attack only seed cones. Consequently, they would have little pest potential on commercially important trees. *Ernobius nigrans* and *Pa. conicola* could also be considered but their biology and effect on seed production are not well known, and more information would be needed for an assessment. Host-specificity screening of the candidate species would be required to verify their host range. All these species are capable of dispersal by flight, but multiple releases covering all affected areas would probably be necessary to ensure that remote infestations are quickly reached.

Whether cone insects can have a significant effect on the population dynamics of wilding *P. contorta* is of primary relevance for the consideration of a biocontrol programme. It is not known which level of seed destruction would be required to achieve a sufficient reduction of spread and population size of wilding pines. Few weed biocontrol programmes have been concerned with trees and none with conifers (Julien 1992), but perennial plants that reproduce with seed are generally considered good targets for biological control (Crawley 1989; Harley and Forno 1992). The fecundity of the exotic leguminous tree *Sesbania punicea* (Cav.) Benth. in South Africa is reduced by over 99% by two introduced biocontrol agents, a stem-miner and a seed-feeder (Hoffmann and Moran 1992). Insects that feed on reproductive structures can achieve, by themselves, successful control of weeds. A seed head-feeding weevil is responsible for one of the most successful weed biocontrol projects, against the thistle *Carduus nutans* in Canada (Crawley 1989). However, significant effects of inflorescence-feeding insects on the host plant population are possible only when

recruitment is seed limited and not limited by a lack of suitable microsites or other post-dispersal factors (Crawley 1989). Wilding pines are likely to be seed limited because of their comparatively short-lived seed bank (Ledgard 1998) and ample availability of suitable microsites in many high country regions.

A model of the effects of herbivores on the abundance of Scotch broom suggests that a 75% reduction in seed production can have a dramatic impact (Rees and Paynter 1997), but a model for knapweed predicts that a 99.5% reduction would be necessary (Cloutier and Watson 1990). It remains to be determined whether cone insects of *P. contorta* could have such an effect, particularly because high levels of damage are rarely seen in its native range. However, this notion is based on a few, mostly small-scale, studies (see Table 1). Also, damage by insects that cause abortion of young cones such as *Co. ponderosae* may be underestimated if an assessment is made only on mature cones (Miller and Ruth 1989). Ideally, life-table studies should be carried out to obtain better estimates of the action of natural enemies throughout the life cycle of cones. Furthermore, cone insects probably cause more damage when they are released from their natural enemies, as would be the case if they were introduced for biological control.

RISKS AND CONFLICTS OF INTEREST

The introduction of cone insects to reduce the spread of wilding pines would probably be unpopular with those concerned about the production of pine seeds for afforestation. Almost all of the pine seed required in New Zealand are produced domestically in seed orchards or seed stands (Vincent 1993). Future planting of *P. contorta*, however, will probably be minimal because of its weed potential and relatively slow growth (Miller and Ecroyd 1987). The introduction of cone insects as biocontrol agents against this tree would therefore be tolerable, provided that the agents are sufficiently host-specific; that is economically important species as well as native trees should not be attacked. Two of the most promising biocontrol candidates, *Pissodes validirostris* and *Co. ponderosae*, would most certainly infest cones of *P. nigra* and *P. ponderosa*, respectively, which have minor importance as plantation species in the South Island high country. This could be problematic because the output from seed orchards could be adversely affected. However, seed orchards are usually small stands that can be protected from insect damage when a cone crop is desired for harvest (Turgeon *et al.* 1994). The establishment of seed orchards on off-shore islands could also be considered to escape, at least temporarily, introduced cone insects. Furthermore, the development of alternative methods for obtaining planting stock including cuttings and somatic embryogenesis could replace the supply from seed. The attack of cones of *P. nigra* and *P. ponderosa* outside of seed orchards could be desirable because these pines are also spreading, although self-established stands of these species could potentially be of interest for future harvesting. The production of pine nuts will probably remain of limited scope in New Zealand (Ledgard 1995) and conflicts of interest are not expected. Attack of any native plants by biocontrol agents against wilding pines is highly unlikely to occur, provided that host-specific agents are used, because there are no native Pinaceae in New Zealand.

A possible undesirable side effect of the introduction of pine cone insects is related to their role as potential vectors of the pine pitch canker fungus, *Fusarium subglutinans* f. sp. *pini* (Wollenw. and Reink) Nelson, Toussoun and Marasas. The disease caused by this fungus has caused much concern because it often kills infected trees and aggressively extends both its geographical and host ranges (Storer *et al.* 1997). Originating in the southeastern USA, it was first reported in California in 1987, where it has spread to *P. radiata*, *P. contorta contorta*, eight other pine species and *Ps. menziesii*, and has also been reported from Mexico, Japan and South Africa. The major vectors are cone and bark beetles (Storer *et al.* 1997), but spittle bugs (Homoptera: Cercopidae) can also transmit the disease (A. Storer, pers. comm.). The importation of disease-free agents is a relatively simple process, but the addition of passive vectors to the limited guild of pine borers that are already established in New Zealand could cause concern if the disease established at a later date.

CONCLUSION

The introduction of cone insects could reduce the rate of spread of wilding *P. contorta*. There are several cone insects which can have a considerable impact on the numbers of seed produced and are sufficiently host-specific to avoid significant non-target effects. Certainly, host-specificity screening and further investigations on the biology and impact of potential agents in their home range would be necessary before any introductions could be considered further. A better understanding of the phenology of cone production and the seed bank would also be required, and the potential role of agents as disease vectors needs evaluation. Modelling the effects of cone insects on seed production and the rate of spread of *P. contorta* under New Zealand conditions could provide an estimate of the likelihood of success. Input from the forest industry in New Zealand is critical.

Biological control with cone insects cannot be seen as a panacea, however, because it would be unlikely to resolve the problem of wildings completely. To achieve this, a very high proportion of seed would have to be destroyed. Thus, an integrated approach to managing invasive pines is necessary (Hobbs and Humphries 1995; Richardson and Higgins 1998). This could include various methods of suppressing new and existing wildings as well as improving the awareness of landholders and the public to include wilding control into regular land management practices. Appropriate actions are urgent because the spread and establishment of wilding pines will likely expand rapidly and further delays will complicate successful control.

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REFERENCES

- Annala, E., 1975. The biology of *Pissodes validirostris* Gyll. (Col., Curculionidae) and its harmfulness, especially in Scots pine seed orchards. *Metsäntutkimuslaitoksen Julkaisu* 85: 1-95.
- Benecke, U., 1967. The weed potential of lodgepole pine. *Tussock Grasslands Mountain Lands Inst. Rev.* 13: 36-42.
- Blatt, S.E. and Borden, J.H., 1996. Distribution and impact of *Leptoglossus occidentalis* Heidemann (Hemiptera: Coreidae) in seed orchards in British Columbia. *Can. Entomol.* 128: 1065-1076.
- Cloutier, D. and Watson, A.K. 1990. Application of modelling to biological weed control. Pp. 5-16 In: Proceedings VII Int. Symp. Biol. Contr. Weeds, March 1988, Rome, Italy. E.S. Delfosse (Ed.); Istituto Sperimentale Patologia Vegetale, Ministero Agricoltura Foreste, Rome, Italy.
- Cock, M.J.W., 1986. Requirements for biological control: an ecological perspective. *Biocontrol News Information* 7: 7-16.
- Crawley, M.J., 1989. Insect herbivores and plant population dynamics. *Annu. Rev. Entomol.* 34: 531-564.
- de Groot, P., Turgeon, J.J. and Miller, G.E., 1994. Status of cone and seed insect pest management in Canadian seed orchards. *For. Chron.* 70: 745-761.
- Graeme, A., 1997. Pulling pines on Ruapehu. *Forest & Bird, May 1997*: 34-37.
- Harley, K.L.S. and Forno, I.W., 1992. Biological Control of Weeds: a Handbook for Practitioners and Students. Inkata Press, Melbourne. 74 pp.
- Hedlin, A.F., Yates III, H.O., Tovar, D.C., Ebel, B.H., Koerber, T.W. and Merkel, E.P., 1980. Cone and Seed Insects of North American Conifers. Canadian Forestry Service; United States Department of Agriculture, Forest Service; Secretaría de Agricultura y Recursos Hidráulicos, Mexico. 122 pp.
- Hobbs, R.J. and Humphries, S.E., 1995. An integrated approach to the ecology and management of plant invasions. *Conserv. Biol.* 9: 761-770.
- Hoffmann, J.H. and Moran, V.C., 1992. Oviposition patterns and the supplementary role of a seed-feeding weevil, *Rhyssomatus marginatus* (Coleoptera: Curculionidae), in the biological control of a perennial leguminous weed, *Sesbania punicea*. *Bull. Ent. Res.* 82: 343-347.

- Hunter, G.G. and Douglas, M.H., 1984. Spread of exotic conifers on South Island rangelands. *N.Z. J. For.* 29: 78-96.
- Julien, M.H., 1992. Biological Control of Weeds: a World Catalogue of Agents and their Target Weeds. CAB International, Wallingford, Oxon, UK. 186 pp.
- Kay, M., 1994. Biological control for invasive tree species. *N.Z. For.* 39: 35-37.
- Keen, F.P., 1958. Cone and seed insects of western forest trees. *U.S. Dept. Agric., Tech. Bull.* 1169: 1-168.
- Ledgard, N.J., 1988. The spread of introduced trees in New Zealand's rangelands - South Island high country experience. *J. Tussock Grasslands Mountainlands Inst.* 44: 1-7.
- Ledgard, N.J., 1995. Pine nuts in N.Z. *Tree Cropper, March* 1995: 18-22.
- Ledgard, N.J., 1998. The spread of lodgepole pine (*Pinus contorta*) in New Zealand. *For. Ecol. Managem.* (submitted).
- Lyons, L.A., 1957. Insects affecting seed production in red pine. II. *Dioryctria disculsa* Heinrich, *D. abietella* (D. and S.), and *D. cambiicola* (Dyar) (Lepidoptera: Phycitidae). *Can. Entomol.* 89: 71-79.
- McFadyen, R.E.C., 1998. Biological control of weeds. *Ann. Rev. Entomol.* 43: 369-393.
- Miller, G.E. and Ruth, D.S., 1989. The relative importance of cone and seed insect species on commercially important conifers in British Columbia. Pp. 25-34 In: Proceedings Cone and Seed Insect Working Party Conference, Working Party S2.07-01, IUFRO, June 1988, Victoria, B.C., G.E. Miller (Ed.); Forestry Canada, Pacific Forestry Centre, Victoria, B.C.
- Miller, J.T. and Ecroyd, C.E., 1987. Introduced forest trees in New Zealand: recognition, role and seed source. 2. *Pinus contorta* Loudon - contorta pine. *FRI Bull.* 124: 1-12.
- New, T.R., 1984. A Biology of Acacias. Oxford University Press, Melbourne. 153 pp.
- Purey-Cust, J. and Hammond, D.R., 1995. A condensed history of forestry in New Zealand. Pp. 26-29 In: Forestry handbook, D.R. Hammond (Ed.); N.Z. Inst. For., Christchurch, New Zealand.
- Rees, M. and Paynter, Q., 1997. Biological control of Scotch broom: modelling the determinants of abundance and the potential impact of introduced insect herbivores. *J. Appl. Ecol.* 34: 1203-1221.
- Richardson, D.M. and Higgins, S.I., 1998. Pines as invaders in the southern hemisphere. Pp. 450-473 In: Ecology and Biogeography of *Pinus*, D.M. Richardson (Ed.); Cambridge University Press, Cambridge.
- Ruckes, H., 1963. Cone beetles of the genus *Conophthorus* in California (Coleoptera: Scolytidae). *Pan-Pacific Entomol.* 39: 43-50.
- Stark, R.W. and Borden, J.H., 1965. Life history of *Choristoneura lambertiana subretiana* Obraztsov (Lepidoptera: Tortricidae) attacking lodgepole pine. *Can. Entomol.* 97: 684-690.
- Storer, A.J., Gordon, T.R., Wood, D.L. and Bonello, P., 1997. Pitch canker disease of pines: current and future impacts. *J. For.* 95: 21-26.
- Turgeon, J.J., Roques, A. and de Groot, P., 1994. Insect fauna of coniferous seed cones: diversity, host plant interactions, and management. *Annu. Rev. Entomol.* 39: 179-212.
- Vincent, T.G., 1993. Supply of improved radiata pine seed. *N.Z. For.* 38: 45-48.
- Waage, J.K. and Greathead, D.J., 1988. Biological control: challenges and opportunities. *Phil. Trans. R. Soc. Lond.* 318: 111-128.
- Wheeler, N.C. and Critchfield, W.B., 1985. The distribution and botanical characteristics of lodgepole pine: biogeographical and management implications. Pp. 1-13 In: Lodgepole pine - the species and its management. Symposium proceedings, May 1984, Spokane, WA and Vancouver, B.C., D.M. Baumgartner, R.G. Krebill, J.T. Arnott and G.F. Wheetman (Eds.); Washington State University, Pullman, WA.