

Predicting the vulnerability of New Zealand radiata pine plantations to the European pine weevil

D. WAINHOUSE^{1*}, S. REAY² AND M. KAY³

¹ Forest Research, Alice Holt Lodge, Alice Holt, Farnham, Surrey, UK

² Silver Bullet Forest Research Ltd, Auckland, New Zealand

³ Ensis-Scion, Rotorua, New Zealand

*Corresponding author. E-mail: david.wainhouse@forestry.gsi.gov.uk

Summary

The European pine weevil, *Hyllobius abietis*, is an important pest of temperate conifers and a significant biosecurity threat to countries such as New Zealand (NZ) where commercial forestry is largely dependent on pine monoculture. The economic impact of this insect is determined by its abundance and the degree of resistance of young pines to adult feeding. Assessing the likely impact of pine weevil in the event of accidental introduction is an important part of contingency planning. Resistance of 1- to 2-year-old trees was assessed by measuring the size of resin ducts within bark of the main stem and the mass of resin flowing from simulated feeding damage. Resin flow relative to duct area was much lower in radiata pine than in Corsican pines that are resistant to weevil feeding in the UK, indicating that NZ radiata pine transplants are likely to be highly susceptible. Local population size is influenced by the availability of pine root stumps after clearfelling. The short rotation of radiata pine and a likely shorter weevil generation time could increase weevil abundance and damage relative to the UK. However, larvae are likely to face competition from previously introduced bark beetles, and possibly native fungi, that rapidly exploit the bark of root stumps after felling. In particular, competition with *Hylurgus ligniperda*, which has an early spring flight and potential for two generations per year, is likely to reduce the number of weevils emerging from root stumps. Overall, pine weevil is likely to have less economic impact in NZ than in northern Europe.

Introduction

The European pine weevil, *Hyllobius abietis* (L.) (Coleoptera: Curculionidae), is a major pest of conifers in Europe (Leather *et al.*, 1999; Lieutier *et al.*, 2004) and as such, a recognized threat to temperate conifer plantations in Australasia (Ohmart, 1980). In New Zealand (NZ), where commercial forestry is based almost exclusively on monocultures of radiata pine, *Pinus radiata* D. Don, pine weevil is a key target of biosecurity measures and determining its likely impact in the event of accidental introduction is an important part of contingency planning.

Pine weevil is a 'silvicultural' pest because its greatest impact is in plantations managed on a cycle of clearfelling and replanting where the abundant roots and associated stumps (root-stumps) of the conifers in which they breed can result in large local populations (Eidmann, 1979, 1985; Långström and Day, 2004). At recent clearfell sites, weevils oviposit in the root-stumps over the summer. Pine and spruce are the main larval hosts, but other conifers are occasionally used and weevils may also breed in logs or windblown trees where bark is in contact with the ground.

On root-stumps, the larvae feed on the bark below ground where they develop over one or more growing seasons, depending on the seasonal timing of oviposition and soil temperatures. The number of weevils that eventually emerge is influenced by the size of the root-stump and the extent to which bark has been utilized by decay fungi (von Sydow, 1993) or competing insects.

The main economic impact occurs when adult pine weevils emerge from root-stumps after the clearfell sites have been replanted and feed on the bark of the main stem of the young plants, often girdling them and causing significant mortality. Other food sources are also utilized including the bark on twigs of established conifers near the emergence site or after dispersal to locate new clearfell oviposition sites (Nordenhem, 1989; Örlander *et al.*, 2000; Wainhouse *et al.*, 2004). In some regions, feeding on roots in the humus layer in conifer stands also seems to be important (Wallertz *et al.*, 2006). Most newly emerged weevils are unable to fly and have an immature reproductive system (Nordenhem, 1989), so this post-emergence 'maturation' feeding is essential for egg development and possibly also for wing muscle development (Tan, 2006). The length of

the pre-ovipositional period and fecundity are affected by the nutritional 'quality' of the food, of which the nitrogen (N) content is an important part (Wainhouse *et al.*, 2004). In southern Britain, adult weevils typically disperse to oviposition sites in late spring (May) when most females are already reproductively mature (Tan, 2006).

The level of damage sustained by transplants prior to dispersal depends largely on their susceptibility and on weevil population size. Young conifers vary in their ability to resist weevil attack, both between and within species, and in Europe transplants can remain vulnerable for 2 or more years after planting. Resistance expression is dependent on the distribution and capacity of the resin duct system within the stem bark of transplants and the amount of resin flowing from ducts damaged by weevil feeding (Wainhouse *et al.*, 2005). Differences in resistance between individual trees of a particular species are influenced by plant size because duct size is related to stem diameter and by age-related differences in the amount of resin synthesized (Wainhouse *et al.*, 2009). Resistant trees are recognized not by the absence of feeding but by the fact that it tends to be restricted to the outer bark, minimizing damage to the cambium, reducing the probability of girdling and increasing the likelihood of effective wound repair.

In the UK, the relative resistance of young Corsican pine, *Pinus nigra* ssp. *laricio* Maire, and Sitka spruce, *Picea sitchensis* (Bong.) Carr. has been assessed by measuring the flow of resin from resin ducts and relating it to weevil feeding damage (Wainhouse *et al.*, 2005, 2009). This relationship can be used to assess the degree of plant resistance in the absence of weevil bioassays by comparing duct size and resin flow with that of trees that express resistance.

Radiata pine growing in southern Europe appears to be moderately susceptible to pine weevil attacks (Zas *et al.*, 2008) but little is known of the relative susceptibility of radiata pine in NZ where this tree has been the subject of an intensive breeding programme since the 1980s (Vincent, 1998; Jayawickrama and Carson, 2000). In this paper, we assess the relative resistance of improved radiata pine seedlings and cuttings, estimate the likely voltinism and consider how weevil populations are likely to develop within the context of NZ plantation forestry.

Materials and methods

Resistance of young Pinus radiata

Assays of resin production in seedlings and cuttings of radiata pine typical of those used in reforestation were used to assess their likely resistance to pine weevil feeding. Seedlings and cuttings from a commercial nursery (Te Ngae Nursery, Rotorua) and seedlings from Scion Research Nursery were used in experiments that were done at Scion Research (Rotorua, NZ). All trees were the product of a tree improvement programme in which selection had occurred for improved growth and form and in some cases also *Dothistroma* resistance. Seedlings were sown in spring (September–October) 2005 and subsequently undercut,

and most had been mechanically topped to a height of ~30 cm as is standard operational practice. Secondary cuttings, i.e. with no terminal bud, were taken in 2005 from hedged plants and after planting out, new extension growth from side buds was subsequently topped to a total plant height of ~30 cm. Seedlings and cuttings were potted in 1.5-l pots in June 2006 and transferred to an unheated polyhouse.

Seedlings from seven different lines were ~1-year old at the time of assessment in November to December 2006, the age at which they would normally be used for replanting, and current spring shoot extension was underway. The stems of original cuttings (~10 cm long) from three different lines were ~2 years old and had been taken from hedged plants that were up to 3 years old. Trees for assay were selected at random and watered to runoff ~24 h before assessment and allowed to equilibrate to ambient laboratory temperature. Measurements were made on the 1-year-old growth increment (GI 1) of seedling plants and on the 2-year-old original stem cutting from which needles had been removed (Figure 1). In the middle of each GI, the stem was wrapped with a pre-weighed 2- to 3-cm-wide strip of transparent polyvinyl chloride (PVC) film (Clingfilm®). The stem was girdled with a scalpel cut that penetrated through the several layers of PVC and underlying bark to the xylem. Resin flowing from the wound was trapped in the layers of PVC which, after 2 h were removed, weighed and the mass of resin determined. On a cross-section of the GI where resin flow was measured, stem diameter and the number and area of resin ducts were determined.

The number and size of ducts and the flow of resin was compared with published data on measurements on GI 1 of susceptible 1-year-old and resistant 2-year-old Corsican pine (Wainhouse *et al.*, 2009).

Soil temperatures in Eastern England and in central North Island NZ

Seasonal variation in soil temperature at a depth of 20 cm was obtained from the UK Meteorological Office for a location near Thetford in south-eastern England. Comparable data for Whakarewarewa and Taupo in NZ were obtained from the NZ Meteorological Service records, from which temperatures at 20 cm were estimated from the mean of those at 10 and 30 cm. The number of day degrees (DD) above 5°C, the developmental threshold for the pine weevil estimated from data in Christiansen, (1971a) was determined for the period May to October in the UK and November to April in NZ.

Nitrogen content of radiata pine bark

The N content of different sources of radiata pine bark on which weevils could feed was determined to assess the likely nutritional quality for weevils. Samples of bark from transplants, twigs from the canopy of trees and root-stumps below ground were taken from compartments in Kaingaroa forest, Central North Island, NZ, as follows: the oldest GI of nine 1-year-old trees planted in the previous dormant

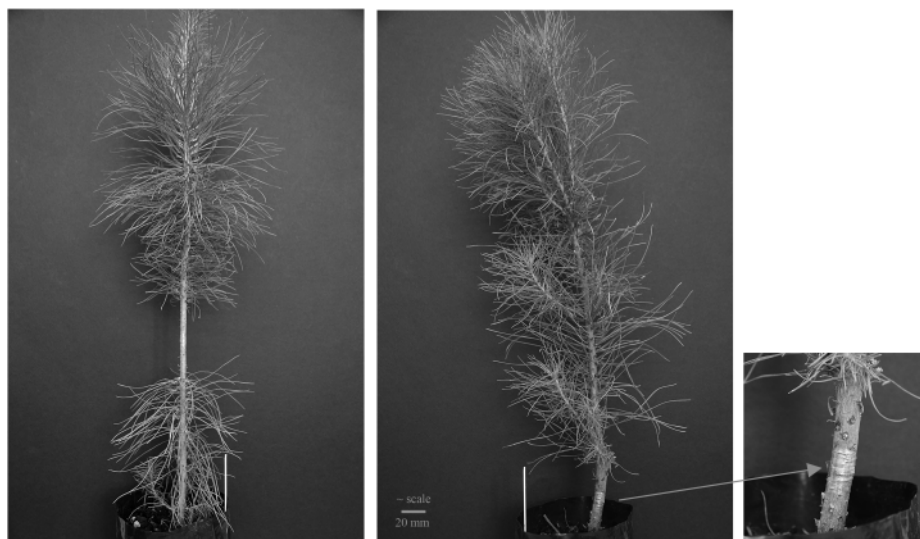


Figure 1. Measurement of resin flow on experimental plants of radiata pine. Seedling (left) ~1-year old with current spring shoot extension underway. Cutting (right) with previous season's growth 'topped' to ~30 cm and with current spring shoot extension. Resin flow was measured in the middle of the 1-year-old growth increment of the seedling and on the original 2-year-old stem cutting (inset) (see text).

season, five root-stumps from a recent clearfell that appeared to be unutilized by insects or fungi and the 2-year-old GI from a branch of nine semi-mature trees. Samples were stored at -18°C prior to analysis. Bark was removed from transplants and twigs and that from three individual trees pooled to give three replicate samples. Inner bark samples from the five root-stumps were analysed individually. Nitrogen content was determined by Vertitec Laboratories (Rotorua), using a modified Dumas method on a Leco CNS-2000 analyser.

Statistical analysis

Data on Corsican pine resin ducts from Wainhouse *et al.* (2009) had been analysed using general linear models in the GenStat statistical package (Payne, 2007). Data from measurements on radiata pine were analysed by linear regression using Statistica (StatSoft, 1995) after log transformation.

Results

Resistance of young *Pinus radiata*

Relationships between the variables (number of resin ducts, resin mass, resin duct area and stem diameter) were similar for seedlings and cuttings and data were combined for regression analysis of ln-transformed variables. The regressions were plotted with the comparable published data for Corsican pine (Figure 2) (Wainhouse *et al.*, 2009). In radiata pine, there were significant relationships between the number of resin ducts and stem diameter ($R^2 = 39.9$,

$P < 0.001$) (Figure 2a), resin duct area and stem diameter ($R^2 = 54.2$, $P < 0.001$) (Figure 2b) and between resin mass and resin duct area ($R^2 = 22.3$, $P < 0.001$) (Figure 2c). The number of resin ducts and duct area tended to increase more rapidly with diameter than in Corsican pine, but total duct area was much lower in the smaller diameter trees. The most important relationship from the point of view of weevil resistance was resin flow relative to duct area. In radiata pine, resin flow from both 1-year-old seedlings and 2-year-old cuttings was similar to that of the susceptible 1-year-old Corsican pine and was much lower than that of the resistant 2-year-old pines (Figure 2c).

Soil temperatures in Eastern England and in central North Island NZ

Seasonal temperature variation in the soil at a depth of 20 cm for a location near Thetford in south-eastern England and for Whakarewarewa and Taupo in NZ are shown in Figure 3. The estimated DD totals above 5°C for each location were, respectively, 1803, 2332 and 2149.

Nitrogen content of radiata pine bark

The nitrogen content of the different sources of radiata pine bark (Figure 4) was compared with data from Scots and Corsican pine in the UK published by Tan (2006). The N content of root and transplant bark from NZ was generally lower than that of published estimates of comparable samples from pines in the UK. In contrast, twig samples were broadly similar in their N concentration.

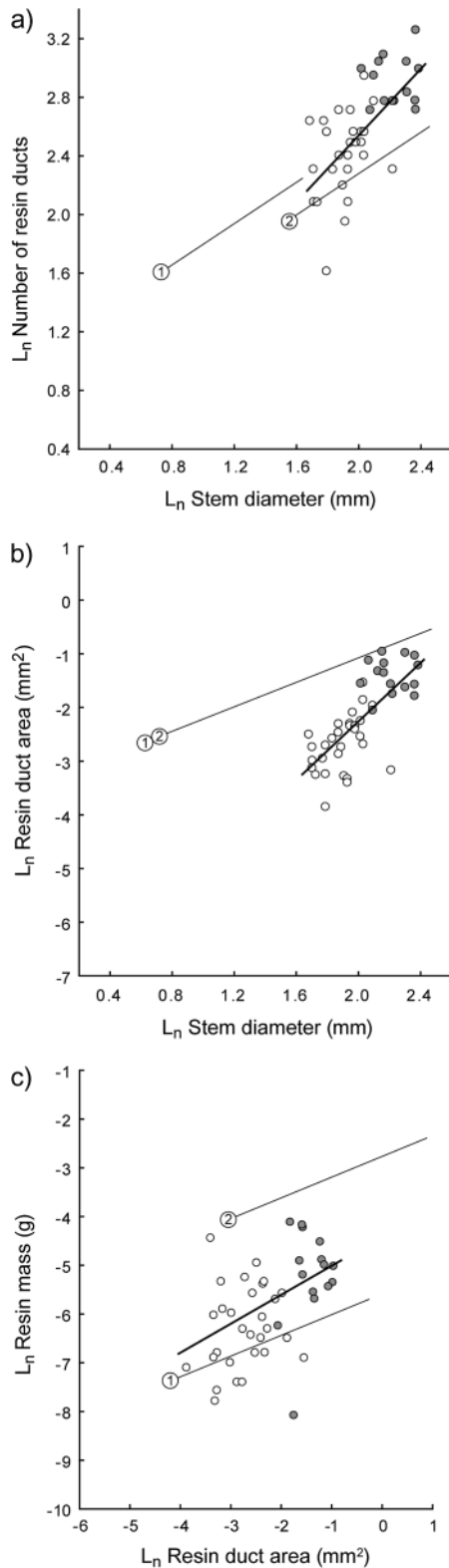


Figure 2. Variation in the number and area of resin ducts and duct area in relation to the diameter of the stems of radiata pine seedlings (○) and cuttings (●). Regressions lines for growth increment 1 for 1- (1) and 2-year-old (2) Corsican pine in the UK are also shown (see text).

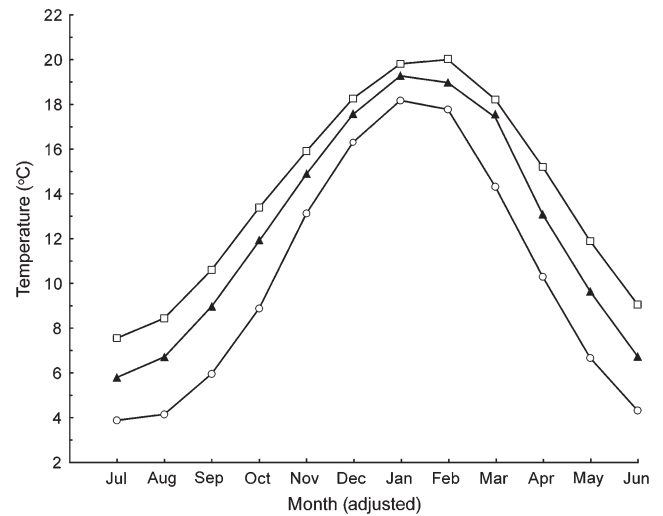


Figure 3. Monthly mean soil temperatures at a depth of 20 cm for locations near Thetford, UK (1989–2007), (○), and Whakarewarewa (□) and Taupo (▲), NZ (1951–1970). Values for NZ were means of 10 and 30 cm depth. Monthly values for UK were reassigned to seasonally equivalent months in NZ.

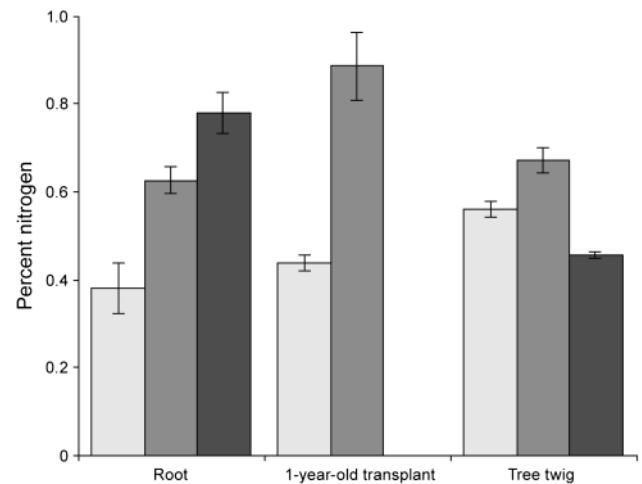


Figure 4. Per cent nitrogen content of bark of roots of felled mature tree, transplants and twigs from large trees. Bars are standard errors. Radiata pine (□). Data for Scots pine (□) and Corsican pine (■) from Tan (2006).

Discussion

In radiata pine, the positive relationship between resin ducts, and the resin they contain, and plant size indicates that young trees are likely to become more resistant as their size increases. However, the amount of resin flow relative to duct area both in 1-year-old seedlings and 2-year-old cuttings was similar to that of 1-year-old Corsican pine that are susceptible to pine weevil (Wainhouse *et al.*, 2009). In Corsican pine, 2-year-old transplants with a lower stem diameter >7 mm are considered to be relatively resistant to pine weevil, but in more susceptible species,

transplants should have a minimum diameter exceeding 10 mm for them to express some resistance to weevil feeding (Thorsen *et al.*, 2001; Wallertz *et al.*, 2005; Wainhouse *et al.*, 2009). The radiata pine seedlings and cuttings used in the present experiments had mean diameters of 6.7 and 9.3 mm, respectively. Our assessment of resin flow indicates that these plants, which were typical of those used in restocking programmes, are likely to be highly susceptible to weevil feeding in the first year after planting out. Their subsequent rapid growth, characteristic of this species in NZ, suggests that their diameter would normally exceed 10 mm during the second growing season, after which they should be relatively resistant.

In Europe, the development rate of larvae is influenced by soil temperatures and host species so that the life cycle can take from <1 to 2 or more years. Pine is considered to be the natural host, on which larvae develop more quickly than on other conifers (Bejer-Petersen *et al.*, 1962; Thorpe and Day, 2002). Development on pine may sometimes be completed in a single season, with adults emerging in the autumn after spring oviposition, though more commonly emergence occurs in the spring or autumn of the following year (Leather *et al.*, 1999; Wainhouse *et al.*, 2007).

When the life cycle is uninterrupted by a quiescent period in the last larval instar, DD above 5°C for development from egg to adult can be estimated from data in Christiansen (1971a), Novák (1965 cited in Christiansen) and Thorpe and Day (2002) as 1766, 2033 and 1350, respectively, giving an estimated mean of 1716 DD. Development in some areas of NZ would therefore be uni-voltine, as it can be in southern England. However, the higher rates of DD accumulation at the two NZ sites suggest that emergence could occur within a single season. After emergence, the rate of reproductive development, and therefore the length of the pre-oviposition period, is influenced by the nitrogen (N) content of the bark. However, only the relatively low concentration of 0.3–0.4 per cent would be limiting for adult pine weevil (Wainhouse *et al.*, 2004). The N content of NZ ash soils is considered to be low by international standards (Gibbs, 1968) though effects on conifers may be ameliorated by mycorrhizae (Fisher and

Stone, 1969). Our limited survey of radiata pine bark from different sources suggests that values are similar to those reported elsewhere, so that the length of the pre-oviposition period in radiata pine plantations is likely to range from 2 to 6 weeks (Wainhouse *et al.*, 2004). Adults are in fact relatively long lived and may undergo a second cycle of oogenesis (Christiansen, 1971b) and may also feed on the bark of root-stumps during oviposition or on the finer roots (Leather *et al.*, 1999; Örlander *et al.*, 2001).

The size of the local population emerging from clear-fells is an important determinant of damage on replanted sites. In NZ, rotation lengths of ~30 years are much shorter than the 50–70 years typical of pine plantations in the UK. In addition, the more frequent cycles of clearfelling and replanting have the potential to increase the size of the population available to colonize clearfells with a resultant increase in damage to transplants. This would, however, depend on the extent to which larvae were able to utilize fully the root-stump breeding resource. In exploiting the inner bark on pine root-stumps in the UK, *H. abietis* larvae can face competition from the larvae of bark beetles, *Hylastes* spp., and cerambycids as well as from fungi. For example, when the basidiomycete *Phlebiopsis gigantea* (Fr.) Jül is applied to the cut surface of pine stumps for biocontrol of *Heterobasidion annosum* (Fr.) Bref, it can colonize significant areas of bark which become unsuitable for larval feeding (Skrzecz, 1996, 2001).

In NZ, the bark on root-stumps is exploited by two introduced bark beetles, *Hylastes ater* (Paykull) and *Hylurgus ligniperda* (F.). These species often co-occur but only *H. ater* causes maturation feeding damage to transplants. The competitive interactions between them for the inner bark of root-stumps have had significant effects on their life cycle (Reay and Walsh, 2001). For example, following the introduction of *H. ligniperda* in the 1970s (Bain, 1977), peak flight activity of *H. ater* in central North Island appears to have changed from mid-summer to late autumn (April). *Hylurgus ligniperda* now dominates exploitation of recent clearfells during the spring and summer period (October–February) and may have two generations per year, as it does in southern Europe (Fabre and Carle, 1975; Reay



Figure 5. Root stumps of *Pinus radiata* within a year of clearfelling at Kinleith forest, Tokoroa, NZ. Bark has been utilized by *Hylurgus ligniperda*, *Hylastes ater* and unidentified fungi. Competition for the bark resource on radiata pine root-stumps could limit population build-up of pine weevil on clearfell sites (see text).

and Walsh, 2001). In Chile, where these two bark beetles also co-occur, *H. ligniperda* flies earlier than *H. ater*, which together with its capacity for multi-voltinism appears to give it a competitive advantage (Mausel *et al.*, 2007). One effect of this in NZ is that transplants, which are not attacked by *H. ligniperda*, suffer less damage as a result of a decline in populations of *H. ater* in areas that are harvested during the spring and summer months (Reay and Walsh, 2001).

These bark beetles are also likely to be important competitors for *H. abietis* (Figure 5). *Hylurgus ligniperda* is absent from the UK, but *H. ater* often colonizes root-stumps before *H. abietis*, utilizing significant areas of bark. The lower flight threshold temperature of these bark beetles (Solbreck and Gyldberg, 1979; Reay and Walsh, 2001; Mausel *et al.*, 2007) and their faster development is likely to give them a competitive edge in exploiting root-stumps in the presence of *H. abietis*. Early colonization of root-stumps by *H. ligniperda*, its more rapid development and its demonstrated effect on *H. ater* suggest that this bark beetle is likely to reduce significantly the availability of inner bark for pine weevil larvae and therefore constrain population size.

In conclusion, the high level of susceptibility of radiata pine transplants suggests that significant damage could occur in the first year after planting, even when weevil population density is relatively low. The timing of replanting relative to weevil emergence, i.e. the length of the fallow period, would also be an important determinant of damage levels. The potential for uni-voltine development and even for completion of the life cycle within a single season is likely to increase weevil abundance, but the rapid utilization of bark on root-stumps by competing insects, and possibly also fungi, suggests that on balance, pine weevil is likely to have less economic impact in NZ than in Northern Europe.

Funding

Support to the first author by the OECD's Cooperative Research Programme: Biological Resource Management for Sustainable Agriculture Systems.

Acknowledgements

Our thanks to Brian Richardson for provision of facilities at Forest Protection and BioSecurity, Scion Research, Rotorua, and to Pam Taylor for supply of experimental material and support. Warwick Brown of Timberlands Ltd, Rotorua, gave helpful advice on commercial plant production and planting regimes. Daegan Inward and Nigel Straw made helpful comments on the manuscript.

Conflict of Interest Statement

None declared.

References

Bain, J. 1977 *Hylurgus ligniperda* (Fabricius) (Coleoptera: Scolytidae). Forest and Timber Insects in New Zealand No. 18. Forest Research Institute, New Zealand Forest Service, Rotorua, New Zealand, 8 pp.

- Bejer-Petersen, B., Juutinen, P., Kangas, E., Bakke, A., Butovitsch, V. and Eidmann, H. *et al.* 1962 Studies on *Hylobius abietis*, L. 1. Development and life cycle in the Nordic countries. *Acta Entomol. Fenn.* 17, 1–106.
- Christiansen, E. 1971a Laboratory study on factors influencing pre-imaginal development in *Hylobius abietis* L. (Col., Curculionidae) *Norsk. ent. Tidsskr.* 18, 1–8.
- Christiansen, E. 1971b Developmental stages in ovaries of pine weevils, *Hylobius abietis* L. (Coleoptera: Curculionidae), present in reforestation areas during the first years after the final felling. *Medd. Nor. Skog.* 28, 389–415.
- Eidmann, H.H. 1979 Integrated management of pine weevil (*Hylobius abietis* L.) populations in Sweden. *Current Topics in Forest Entomology*. Forest Service General Technical Report WO-8 USDA. USDA Forest Service, Washington, DC. pp. 103–109.
- Eidmann, H.H. 1985 Silviculture and insect problems. *Z. Angew. Entomol.* 99, 105–112.
- Fabre, J.-P. and Carle, P. 1975 Contribution à l'étude biologique d'*Hylurgus ligniperda* F. (Coleoptera: Scolytidae) dans le sud-est de la France. *Ann. Sci. For.* 32, 55–71.
- Fisher, R.F. and Stone, E.L. 1969 Increased availability of nitrogen and phosphorous in the root zone of conifers. *Soil Sci. Soc. Am. Proc.* 33, 955–961.
- Gibbs, H.S. 1968 *Volcanic ash soils in New Zealand*. NZ DSIR Information Series No. 65, 39 pp.
- Jayawickrama, K.J.S. and Carson, M.J. 2000 A breeding strategy for the New Zealand radiata pine breeding cooperative. *Silvae Genet.* 49, 82–90.
- Långström, B. and Day, K.R. 2004 Damage, control and management of weevil pests, especially *Hylobius abietis*. In *Bark and Wood Boring Insects in Living Trees in Europe, a Synthesis*. F. Lieutier, K.R. Day, A. Battisti, J.-C. Grégoire and H.F. Evans (eds). Kluwer Academic Publishers. Dordrecht, The Netherlands. pp. 415–444.
- Leather, S.R., Day, K.R. and Salisbury, A.N. 1999 The biology and ecology of the large pine weevil, *Hylobius abietis* (Coleoptera: Curculionidae): a problem of dispersal? *Bull. Entomol. Res.* 89, 3–16.
- Lieutier, F., Day, K.R., Battisti, A., Grégoire, J.-C. and Evans, H.F. 2004 (eds). *Bark and Wood Boring Insects in Living Trees in Europe, a Synthesis*. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Mausel, D.L., Gara, R.I., Lanfranco, D., Ruiz, C., Ide, S. and Azat, R. 2007 The introduced bark beetles *Hylurgus ligniperda* and *Hylastes ater* (Coleoptera: Scolytidae) in Chile: seasonal flight and effect of *Pinus radiata* log placement on colonization. *Can. J. For. Res.* 37, 156–169.
- Nordenhem, H. 1989 Age, sexual development, and seasonal occurrence of the pine weevil *Hylobius abietis* (L.). *J. Appl. Entomol.* 108, 260–270.
- Ohmart, C.P. 1980 Insect pests of *Pinus radiata* plantations: present and possible future problems. *Aust. For.* 43, 226–232.
- Örlander, G., Nordlander, G., Wallertz, K. and Nordenhem, H. 2000 Feeding in the crowns of Scots pine trees by the pine weevil *Hylobius abietis*. *Scand. J. For. Res.* 15, 194–201.
- Örlander, G., Nordlander, G. and Wallertz, K. 2001 Extra food supply decreases damage by the pine weevil *Hylobius abietis*. *Scand. J. For. Res.* 16, 450–454.

- Payne, R.W. (ed). 2007 In *The Guide to GenStat Release 10*. VSN International, Hemel Hempstead.
- Reay, S.D. and Walsh, P.J. 2001 Observations of the flight activity of *Hylastes ater* and *Hylurgus ligniperda* (Curculionidae: Scolytinae) in *Pinus radiata* forests in the central North Island, New Zealand. *N. Z. Entomol.* **24**, 79–85.
- Skrzecz, I. 1996 Impact of *Phlebia gigantea* (Fr.: Fr) Donk on the colonization of Scots pine (*Pinus sylvestris* L.) stumps by the large pine weevil (*Hylobius abietis* L. *Folia Forest. Polon.* **38**, 89–101.
- Skrzecz, I. 2001 Large pine weevil (*Hylobius abietis*) abundance and the extent of damage in plantations established on clearcuts with pine stumps treated with the fungus *Phlebiopsis gigantea* (Fr.: Fr.) Julich. *Folia Forest. Polon.* **43**, 127–142.
- Solbreck, C. and Gyldberg, B. 1979 Temporal flight pattern of the large pine weevil, *Hylobius abietis* L. (Coleoptera, Curculionidae), with special reference to the influence of weather. *Z. Angew. Entomol.* **88**, 532–536.
- StatSoft 1995 *Statistica for Windows*. 2nd edn. StatSoft Inc., Tulsa, OK.
- Tan, J.Y. 2006 Dispersal and Reproduction in the Ecology of the Pine Weevil, *Hylobius abietis* L. (Coleoptera: Curculionidae). Ph.D. thesis, University of Ulster.
- Thorpe, K.V. and Day, K.R. 2002 The impact of host plant species on the larval development of the large pine weevil *Hylobius abietis* L. *Agric. For. Entomol.* **4**, 187–194.
- Thorsen, A., Mattsson, S. and Weslien, J. 2001 Influence of stem diameter on the survival and growth of containerized Norway spruce seedlings attacked by pine weevils (*Hylobius* spp.). *Scand. J. For. Res.* **16**, 54–66.
- Vincent, T.G. 1998 *GFPlusTM*. New Zealand Radiata Pine Breeding Cooperative, Rotorua, New Zealand.
- von Sydow, F. 1993 Fungi occurring in the roots and basal parts of one- and two-year-old spruce and pine stumps. *Scand. J. For. Res.* **8**, 174–184.
- Wainhouse, D., Boswell, R. and Ashburner, R. 2004 Maturation feeding and reproductive development in adult pine weevil, *Hylobius abietis* (Coleoptera: Curculionidae). *Bull. Entomol. Res.* **94**, 81–87.
- Wainhouse, D., Brough, S. and Greenacre, B. 2007 *Managing the pine weevil on lowland pine*. Forestry Commission Practice Note 14. Forestry Commission, Edinburgh, 12 pp.
- Wainhouse, D., Staley, J., Johnston, J. and Boswell, R. 2005 The effect of environmentally induced changes in the bark of young conifers on feeding behaviour and reproductive development of adult *Hylobius abietis* (Coleoptera: Curculionidae). *Bull. Entomol. Res.* **95**, 151–159.
- Wainhouse, D., Staley, J.T., Jinks, R. and Morgan, G. 2009 Growth and defence in young pine and spruce and the expression of resistance to a stem feeding weevil. *Oecologia.* **158**, 641–650.
- Wallertz, K., Nordlander, G. and Örlander, G. 2006 Feeding on roots in the humus layer by adult pine weevil, *Hylobius abietis*. *Agric. For. Entomol.* **8**, 273–279.
- Wallertz, K., Örlander, G. and Luoranen, J. 2005 Damage by pine weevil *Hylobius abietis* to conifer seedlings after shelterwood removal. *Scand. J. For. Res.* **20**, 412–420.
- Zas, R., Sampedro, L., Moreira, X. and Martins, P. 2008 Effect of fertilization and genetic variation on susceptibility of *Pinus radiata* seedlings to *Hylobius abietis* damage. *Can. J. For. Res.* **38**, 63–72.

Received 3 March 2010