C.P. Alexander Review / Revue C.P. Alexander[1]

Biology and management of North American cone-feeding *Dioryctria* species

C.M. Whitehouse, A.D. Roe, W.B. Strong, M.L. Evenden, F.A.H. Sperling

Abstract—Coneworms, *Dioryctria* Zeller (Lepidoptera: Pyralidae), are destructive pests of conifers across North America, and members of several different species groups present significant pest-management challenges in conifer seed orchards. *Dioryctria abietivorella* Grote (*abietella* group) is the most pestiferous *Dioryctria* species in Canada. Despite this status, control tactics are currently limited to broad-spectrum pesticides that threaten non-target species and may result in pesticide resistance. The development of integrated pest management programs targeting *Dioryctria* species will benefit from a conceptual framework on which to base future research. To create this structure, we review the systematics, evolutionary ecology, and management of cone-feeding North American *Dioryctria* species. Current research suggests that many species boundaries are in need of further revision. Major gaps in our understanding of *Dioryctria* ecology impede the development of integrated pest management tactics. For example, host-generated semiochemicals are important in *Dioryctria* reproduction, although the uses of these cues in host-finding and host acceptance remain unknown. Future research should identify factors that mediate population distribution at landscape (*e.g.*, migration), local (*e.g.*, feeding stimulants), and temporal (*e.g.*, development thresholds) scales.

Résumé—Les pyrales des cônes, *Dioryctria* Zeller (Lepidoptera : Pyralidae), sont des ravageurs destructeurs des conifères dans toute l'Amérique du Nord et les membres de plusieurs groupes différents d'espèces représentent des défis importants de gestion dans les vergers à graines de conifères. *Dioryctria abietivorella* Grote (du groupe d'espèces de *abietella*) est l'espèce de *Dioryctria* la plus dommageable au Canada. Malgré ce statut, les tactiques de lutte se réduisent actuellement à l'utilisation de pesticides à large spectre qui menacent les espèces non ciblées et qui peuvent provoquer de la résistance aux pesticides. La mise au point de programmes de lutte intégrée contre les espèces de *Dioryctria* bénéficierait d'un cadre conceptuel sur lequel baser la recherche future. Afin d'élaborer une telle structure, nous faisons une revue de la systématique, de l'écologie évolutive et de la gestion des *Dioryctria* nord-américains qui se nourrissent de cônes. La recherche actuelle indique que plusieurs des frontières entre les espèces doivent être examinées à nouveau. Il demeure des failles importantes dans notre compréhension de l'écologie des *Dioryctria* qui entravent la mise au point de tactiques de lutte intégrée. Par exemple, les substances sémiochimiques générées par l'hôte sont d'importance pour la reproduction des *Dioryctria*, bien que le rôle de ces signaux dans la recherche

---

Received 26 March 2010. Accepted 25 July 2010.

[1] This series is supported by a fund established in memory of the late Charles P. Alexander. The Entomological Society of Canada uses the fund to support the publication of invited articles or reviews on topics that broaden the scope of *The Canadian Entomologist* and (or) are of current significance to entomology.
Cette série est financée par un fond établi à la mémoire de feu Charles P. Alexander. La Société d'entomologie du Canada utilise les fonds afin de supporter la publication d'articles ou de revues sur invitation portant sur des sujets qui élargissent le champ de *The Canadian Entomologist* et (ou) sont présentement pertinents en entomologie.

C.M. Whitehouse,[2] A.D. Roe, M.L. Evenden, F.A.H. Sperling, Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada T6G 2E9
W.B. Strong, Kalamalka Forestry Centre, British Columbia Ministry of Forests, Vernon, British Columbia, Canada V1B 2C7

[2] Corresponding author (e-mail: cmw7@ualberta.ca).
doi: 10.4039/n10-045

Can. Entomol. **143**: 1–34 (2011)

et l'acceptation des hôtes reste inconnue. Les recherches futures devraient identifier les facteurs qui expliquent la répartition des populations à l'échelle du paysage (par exemple, la migration), à l'échelle locale (par exemple, les stimulants alimentaires) et à l'échelle temporelle (par exemple, les seuils de développement).

[Traduit par la Rédaction]

Introduction

Coneworms, *Dioryctria* (Lepidoptera: Pyralidae), are destructive pests of conifers throughout the Holarctic region. *Dioryctria* species feed on foliage, cambium, and tree wounds; however, they are most economically damaging when they consume ovulate cones of genetically improved trees (Neunzig 2003). Cone-feeders comprise 35 of the 79 species in *Dioryctria*, and these are the most pestiferous Lepidoptera associated with conifer seed cone production (Hedlin *et al*. 1980; Turgeon *et al*. 1994). *Dioryctria* infestations cause substantial economic losses to seed-orchard production of genetically superior conifer seed for reforestation programs (Hedlin *et al*. 1980; Zobel and Talbert 1984).

Despite the pest status of certain cone-feeding *Dioryctria* species, their evolutionary ecology is poorly understood. Evolution in this group is likely driven by the temporal and spatial heterogeneity of cone crops and niche separation of sympatric species. Cone-feeding *Dioryctria* species that exploit highly variable annual seed crops tend to use a wide range of host genera; *Dioryctria* species that feed on less ephemeral tissue types (*e.g.*, cambium) can be restricted to a single host (McLeod and Daviault 1963; Neunzig 2003). Polyphagy, here defined as feeding on more than one conifer genus, is a successful feeding strategy for some *Dioryctria* species and appears to be linked to pest status in the genus. Fir coneworm, *Dioryctria abietivorella* Grote, is the most geographically widespread and pestiferous species of *Dioryctria* in Canada. It exhibits polyphagous feeding habits that vary across its wide geographic range in North America, and in 2004 caused an estimated $1 million Cdn. loss to seed production in seed orchards in southern interior British Columbia (Strong 2005).

Identification of *Dioryctria* species on the basis of morphological characters is difficult and impedes the development of the accurate monitoring tools needed in integrated pest management programs targeting these species. Continuing uncertainties about species limits have complicated the ecological literature on *Dioryctria* (Hedlin *et al*. 1980; Sopow *et al*. 1996; Du *et al*. 2005). Recent molecular and morphological studies (Du *et al*. 2005; Roe *et al*. 2006; Roe and Sperling 2007; Roux-Morabito *et al*. 2008) have begun to clarify the relationships among species within this genus. Continued research on the systematics and life history of *Dioryctria* will enhance the development of integrated pest management programs for these important pests of conifers (Sopow *et al.* 1996; Roe *et al.* 2006; Roux-Morabito *et al.* 2008).

This review presents a synthesis of research completed to date on the systematics, life history, ecology, and management of *D. abietivorella* and other cone-feeding *Dioryctria* species in North America. Turgeon *et al.* (1994) broadly addressed the ecology of cone- and seed-feeding insects and Neunzig (2003) focused on the morphology-based taxonomy of the genus. Here we highlight the interaction of evolutionary relationships and ecological phenomena in the genus and identify the biological information required to develop integrated pest management systems that efficiently target *Dioryctria* pest species.

Systematics, taxonomy, and diversity of *Dioryctria*

Dioryctria (Zeller 1846) is a large, morphologically distinct genus of phycitine moths in the family Pyralidae. Members of the genus are found throughout the Holarctic region, with a handful of species in the Neotropical and Indomalayan regions. Currently the genus contains 79 species, although recent studies suggest the existence of an additional, undescribed species (Du *et al*. 2005; Roux-Morabito *et al.* 2008). Recognition of *Dioryctria* species is difficult, owing to interspecific overlap of diagnostic traits such as wing coloration, genitalic structures, and host association (Sopow *et al.* 1996; Roe and Sperling 2007) (Table 1, Figs. 1–3). Species delimitation therefore requires molecular data (Roe *et al.* 2006) (Table 2) or the identification of novel morphological traits (Simonsen and Roe 2009). Seven species groups were initially proposed in *Dioryctria* to improve identification and understanding of the morphological and behavioural diversity within the genus (Mutuura and Munroe 1972). A number of additional species groups have since been described (Mutuura and Munroe 1974; Wang and Sung 1982; Speidel and Asselbergs 2000; Neunzig 2003), and phylogenetic relationships within and between these groups have been examined more extensively (Du *et al.* 2005; Roe *et al.* 2006; Roux-Morabito *et al.* 2008).

The current hypothesis of relationships among 7 of the 11 species groups was produced using a parsimony analysis of previously published sequence data from mitochondrial cytochrome *c* oxidase I and II genes (COI−COII) (Table 2, Fig. 1). Given the importance of *D. abietivorella* as a pest in Canada, all available representative species in the *abietella* group were included in the analysis, along with representative taxa from the remaining species groups and two species (*D. okui* Mutuura and *D. juniperella* Yamanaka) that have not been assigned to a group (Fig. 1). Consistent with previously published phylogenies (Du *et al.* 2005; Roe *et al.* 2006), the majority of species groups form well-supported monophyletic clades, with the exception of the *auranticella* group (although this conclusion is tentative because of incomplete sampling of species). A monophyletic clade, the "raised scale group", containing three species groups (*zimmermani*, *baumhoferi*, and *ponderosae*) has also been resolved, whereas relationships among other species groups have not been confidently resolved (Fig. 1).

Cone-feeding *Dioryctria* species

Within North America, 40 species of *Dioryctria* have been described. Seventeen of these, constituting seven species groups, are cone-feeders, though some also feed on phloem and foliage (Neunzig 2003) (Table 1, Fig. 1). Larval hosts for most *Dioryctria* species are in Pinaceae; two species specialize on members of Cupressaceae (Table 1, Fig. 1). Many *Dioryctria* species associate with only one or two closely related host-plant species, typically in the genus *Pinus* L. (Pinaceae), but other species are polyphagous (Neunzig 2003; Roux-Morabito *et al.* 2008). The *ponderosae* group (*D. ponderosae* Dyar, *D. okanaganella* Mutuura, Munroe and Ross, and *D. hodgesi* Neunzig) is the only North American species group that lacks cone-feeders.

The abietella *group*

The *abietella* group contains 15 species, most of which have either a Nearctic or a Palearctic distribution. Larvae of members of this group feed on a range of hosts and host tissues. Cone-feeding is the most prevalent feeding habit in the *abietella* group (Table 1, Fig. 1) and many of these species are important economic pests. Minor fore-wing and genitalic characters have been used to identify species, but accurate identification requires information on host-plant association or geographic location (Segerer and Pröse 1997). In recent work, the species limits of a number of *abietella*-group members have been examined using mitochondrial DNA (mtDNA) sequences (Roux-Morabito *et al.* 2008). The combination of all previously published COI−COII sequences for the *abietella* group (Du *et al.* 2005; Knölke *et al.* 2005; Roe *et al.* 2006; Roux-Morabito *et al.* 2008) shows a range of intra- and inter-specific variation among species in the group (Table 2). Specifically, *D. abietella* Denis and Schiffermüeller has high intraspecific variation and fails to form a monophyletic group (Roux-Morabito *et al.* 2008) (Table 2, Fig. 1), contrasting with the low variation in most other species in the group. Phylogenetic results obtained from the European members of the *abietella* group suggest the existence of cryptic species (Roux-Morabito *et al.* 2008). This issue requires further examination.

The most important species in the *abietella* group in Canada, *D. abietivorella*, has a convoluted nomenclatural history that makes interpretation of the literature difficult. Originally, Grote (1878) described the species as *Pinipestis abietivorella*. Two years later, Grote (1880) described a similar species, *P. reniculella*. Subsequent revision of the genus *Dioryctria* by Ragonot (1893) saw these two species

Table 1. Host and tissue use by *Dioryctria* species organized by species group (modified from Coulson and Franklin 1970*a*; Neunzig 2003).

Dioryctria species	Larval host	Tissue used	Citation
***abietella* group**			
abietivorella	Fir species, *Abies* Mill. Spruce species, *Picea* A. Dietr. Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco Jack pine, *Pinus banksiana* Lamb. Lodgepole pine, *Pinus contorta* Douglas *ex* Loudon Red pine, *Pinus resinosa* Aiton Scots pine, *Pinus sylvestris* L. White pine, *Pinus strobus* L.	Healthy cones Damaged second-year cones Needles Shoots Cambium	Heinrich 1956; Lyons 1957; Prentice 1965; Hedlin *et al.* 1980; Neunzig 2003
ebeli	Loblolly pine, *Pinus taeda* L. Longleaf pine, *Pinus palustris* M. Slash pine, *Pinus elliottii* Engelm.	Rust-infested first-year cones Healthy second-year cones Fusiform rust cankers Vegetative buds and shoots Previously infested material	Ebel 1965; Mutuura and Munroe 1979; Hedlin *et al.* 1980; Neunzig 2003
***auranticella* group**			
auranticella	Austrian pine, *Pinus nigra* Arnold Knobcone pine, *Pinus attenuata* Lemmon Ponderosa pine, *Pinus ponderosa* C. Lawson	Male and female flowers Second-year cones	Raizenne 1952; Heinrich 1956; Prentice 1965; Hedlin *et al.* 1980; Pasek and Dix 1989; Neunzig 2003
disclusa	Austrian pine Jack pine Loblolly pine Longleaf pine Mountain pine, *Pinus uncinata* Mill. *Ex* Mirb. Pitch pine, *Pinus rigida* Mill. Red pine Scots pine Virginia pine, *Pinus virginiana* Mill.	Male and female flowers Second-year cones	Farrier and Tauber 1953; Heinrich 1956; Lyons 1957; Munroe 1959; Neunzig *et al.* 1964 ; Prentice 1965; Hedlin *et al.* 1980; Pasek and Dix 1989; Neunzig 2003
rossi	Arizona pine, *Pinus arizonica* Engelm. Durango pine, *Pinus durangensis* Martínez Ponderosa pine	Cones	Munroe 1959; Prentice 1965; Hedlin *et al.* 1980; Neunzig 2003

Table 1 (*continued*).

Dioryctria species	Larval host	Tissue used	Citation
***baumhoferi* group**			
clarioralis	Loblolly pine Longleaf pine Shortleaf pine, *Pinus echinata* Mill. Slash pine	First- and second-year cones Buds	Heinrich 1956; Neunzig *et al*. 1964; Ebel 1965; Hedlin *et al.* 1980; Neunzig 2003
pentictonella	Lodgepole pine Ponderosa pine	Cones Buds	Mutuura *et al.* 1969; Hedlin *et al.* 1980; Neunzig 2003
***erythropasa* group**			
erythropasa	Chihuahua pine, *Pinus leiophylla* Schiede and Deppe var. *chihuahuana* (Engelm.) Shaw	Cones	Heinrich 1956; Hedlin *et al.* 1980; Neunzig 2003
***pygmaeella* group**			
caesirufella	Bald cypress, *Taxodium distichum* (L.) Rich.	Cones	Blanchard and Knudson 1983; Hedlin *et al.* 1980; Neunzig 2003;
pygmaeella	Bald cypress Pondcypress, *Taxodium ascendens* Brongn.	Cones	Heinrich 1956; Hedlin *et al.* 1980; Neunzig 2003
***schuetzeella* group**			
pseudotsugella	Douglas-fir	Cones Cambium	Munroe 1959; Prentice 1965; Mutuura and Munroe 1973; Hedlin *et al.* 1980; Neunzig 2003
reniculelloides	White spruce, *Picea glauca* (Moench) Voss Sitka spruce, *Picea sitchensis* (Bong.) Carrière Engelmann spruce, *Picea engelmannii* Parry *ex* Engelm. Black spruce, *Picea mariana* (Mill.) Britton, Sterns & Poggenb. Colorado spruce, *Picea pungens* Engelm. Douglas-fir Western hemlock, *Tsuga heterophylla* (Raf.) Sarg. Alpine fir, *Abies lasiocarpa* (Hook.) Nutt. Amabilis fir, *Abies amabilis* (Douglas *ex* Louden) Douglas *ex* Forbes Balsam fir, *Abies balsamea* (L.) Mill. White fir, *Abies concolor* (Gord. & Glend.) Lindl. *Ex* Hildebr. Lodgepole pine	Shoots Foliage Cones	MacKay 1943; Heinrich 1956; Munroe 1959; McLeod and Daviault 1963; Prentice 1965; Mutuura and Munroe 1973; Hedlin *et al.* 1980; Neunzig 2003

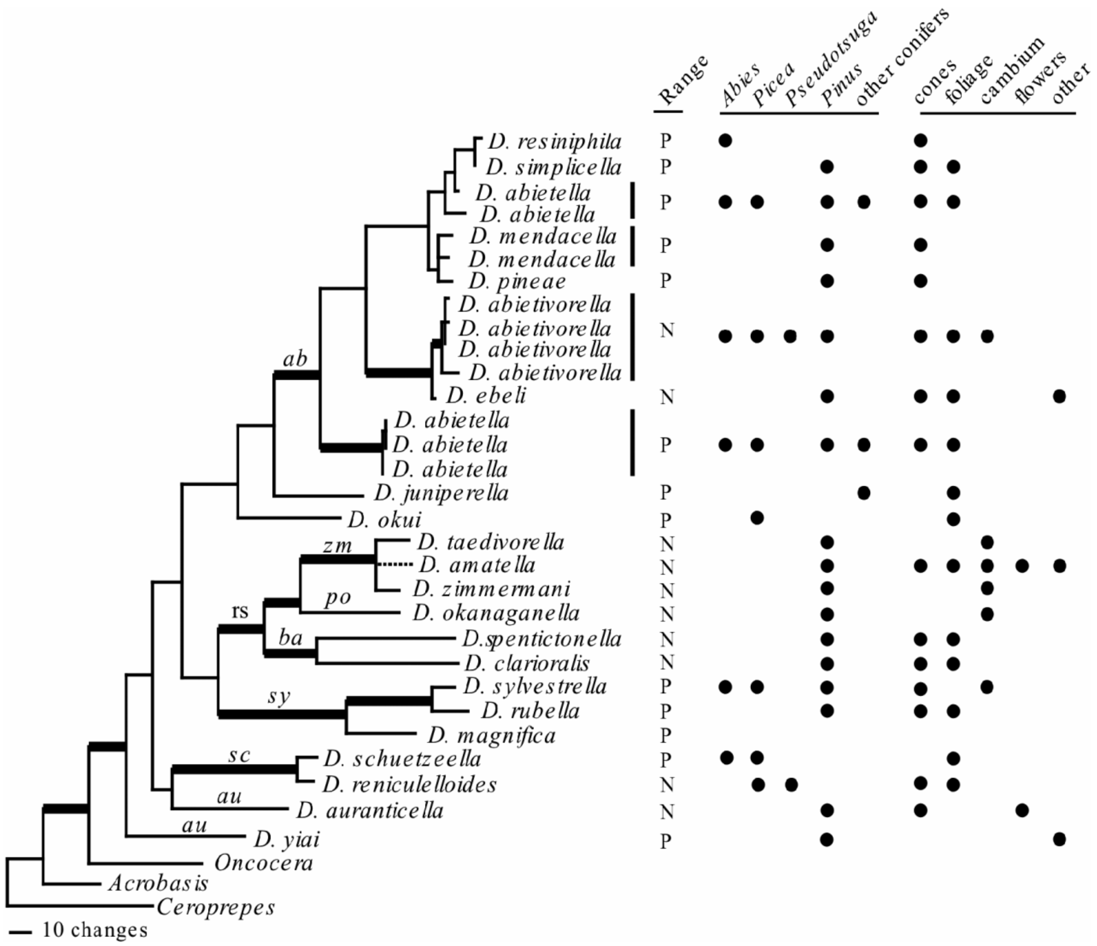
Table 1 (*concluded*).

Dioryctria species	Larval host	Tissue used	Citation
***zimmermani* group**			
amatella	Loblolly pine Longleaf pine Shortleaf pine Slash pine	Rust-infected first-year cones Healthy second-year cones Terminal shoots Fusiform canker galls Buds Flowers Wounds	Heinrich 1956; Neunzig *et al.* 1964; Ebel 1965; Franklin and Coulson 1970*a*, 1970*b*; Hedlin *et al.* 1980; Neunzig 2003
cambiicola	Coulter pine, *Pinus coulteri* D. Don	Cambium Second-year cones Shoots Buds *Peridermium* blister rust canker	Heinrich 1956 ; Lyons 1957 ; Munroe 1959; Mutuura *et al.* 1969; Hedlin *et al.* 1980; Neunzig 2003
merkeli	Loblolly pine Longleaf pine Slash pine	Flowers Shoots Cones	Mutuura and Munroe 1979; Hedlin *et al.* 1980; Neunzig 2003
resinosella	Red pine	Lateral and terminal shoots Cones	Hedlin *et al.* 1981; Mutuura 1982; Neunzig 2003
taedae	Loblolly pine	Cones	Schaber and Wood 1971; Hedlin *et al.* 1981; Neunzig 2003
taedivorella	Loblolly pine	Cones	Neunzig *et al.* 1964
yatesi	Table mountain pine, *Pinus pungens* Lamb.	Cones	Mutuura and Munroe 1979; Hedlin *et al.* 1980; Neunzig 2003

reclassified as *D. abietivorella* and *D. reniculella* (Grote), respectively. Examination of the *D. reniculella* types by Amsel (1962) and Mutuura and Munroe (1973) demonstrated that both holotypes were in fact specimens of *D. abietivorella*, making *D. reniculella* a junior synonym. Earlier, Heinrich (1956) had synonymized *D. abietivorella* with the European *D. abietella* and misidentified a second distinct Nearctic species as *D. reniculella*. In 1959, Munroe reexamined North American specimens identified as *D. abietella* and recognized them as *D. abietivorella*, distinct from the Palearctic specimens, based on fore-wing and genitalic characteristics. After the identity of the *D. reniculella* holotype was clarified (Amsel 1962; Mutuura and Munroe 1973), the North American specimens considered by Heinrich (1956) to represent *D. reniculella* were named *D. reniculelloides* (Mutuura and Munroe 1973), whereas specimens identified as *D. reniculella* prior to Heinrich (1956) were in fact *D. abietivorella*. Finally, a second closely related species, *D. ebeli* (Mutuura and Munroe 1979), was described from the southeastern United States, and much of the earlier literature on *D. abietella* and *D. abietivorella* from that region actually refers to *D. ebeli* (*e.g.*, Ebel 1965; Fatzinger and Asher 1971*b*). Given the taxonomic turmoil surrounding *D. abietivorella*, confirmation of the accuracy of taxonomic names used in the literature is particularly important.

In North America the *abietella* group includes the seed-feeding *D. abietivorella* and *D. ebeli* (Table 1, Fig. 1). The geographic range of *D. abietivorella* extends across southern

Fig. 1. One of two most parsimonious phylograms (length = 1444) based on mitochondrial sequences (cytochrome *c* oxidase I and II; available on GenBank) from exemplar *Dioryctria* species representing major species groups and three outgroups. Thick branches indicate >80% parsimony bootstrap support (100 replicates). Labeled nodes are as follows: *ab, abietella* group; *au, auranticella* group; *ba, baumhoferi* group; *po, ponderosae* group; rs, raised-scale group; *sc, schuetzeella* group; *zm, zimmermani* group. *Dioryctria amatella* (broken line) lacks sequence data but is placed within the *zimmermani* group, based on morphological characteristics. Geographic range (Nearctic (N) or Palearctic (P)), native host, and host-plant tissue are indicated.



Canada and throughout the western United States (Heinrich 1956; Lyons 1957; Munroe 1959; Prentice 1965; Neunzig 2003), whereas the distribution of *D. ebeli* is restricted to the southeastern United States (Mutuura and Munroe 1979; Neunzig 2003). These two species have a surprising lack of genetic variation, despite differences in geographic range and host associations (Roux-Morabito *et al.* 2008) (Tables 1, 2, Fig. 1). This lack of genetic variation suggests extensive gene flow between these two species, possibly because of a recent range expansion or a selective sweep that has driven an advantageous mutation through all populations. To clarify species limits between *D. abietivorella* and *D. ebeli*, a more detailed population genetic analysis is needed. The differences in mtDNA between *D. abietivorella* and *D. abietella* are much greater than those between *D. abietivorella* and *D. ebeli*. Du *et al.* (2005) show a 3.8% uncorrected distance at the COI−COII locus, which further supports the recognition of *D. abietivorella* as distinct from *D. abietella* (Munroe 1959) (Table 2, Fig. 1).

Fig. 2. *Dioryctria abietivorella* (*abietella* group). (*a*) Fertilized egg. (*b*) Larva. (*c*) Adult. (*d*) Infested cone with external accumulation of frass.

Fig. 3. Left fore- and hind- wings of adults of *Dioryctria* species. (*a*) *Dioryctria auranticella* (*auranticella* group). (*b*) *Dioryctria okanaganella* (*ponderosae* group). (*c*) *Dioryctria pseudotsugella* (*schuetzeella* group). (*d*) *Dioryctria cambiicola* (*zimmermani* group). (*e*) *Dioryctria pygmaeella* (*pygmaeella* group).

The auranticella *group*

All North American members of the *auranticella* group, *D. auranticella* Grote, *D. rossi* Munroe, and *D. disclusa* Heinrich, are cone-miners (Table 1, Figs. 1, 3). *Dioryctria auranticella* and *D. rossi* occur sympatrically over most of their ranges between southern British Columbia and New Mexico, although *D. rossi* is also found in western Texas (Heinrich 1956; Neunzig 2003). The economically important *D. disclusa* is found in eastern Canada and in

Table 2. Members of the *Dioryctria abietella* group, with ranges of intra- and inter-specific divergence (uncorrected pairwise distance) of mitochondrial cytochrome *c* oxidase I and II genes shown, when available.

	Intraspecific divergence (%)	Interspecific divergence (%)	Reference
D. abietella Denis and Schiffermüller	**0–4.8**	**1.1–5.0**	Du *et al*. 2005; Roux-Morabito *et al*. 2008
D. abietivorella Grote	**0–0.8**	**0–4.7**	Du *et al*. 2005; Roe *et al*. 2006; Roux *et al*. 2008
D. ebeli Mutuura and Munroe	na	0–4.3	Roux-Morabito *et al*. 2008
D. mendecella Staudinger	**0.1–1.4**	**1.2–4.8**	Roux-Morabito *et al*. 2008
D. pineae Staudinger	0	1.2–4.5	Roux-Morabito *et al*. 2008
D. resiniphila Segerer and Pröse	na	0.8–4.9	Knölke *et al*. 2005
D. simplicella Heinemann (= *D. mutatella* Fuchs and Fazekas)	0	0.8–5.1	Roux-Morabito *et al*. 2008

Note: Values in boldface type are distances for species with overlapping intra- and inter-specific variation.

the eastern and central United States as far west as eastern Texas (Heinrich 1956; Neunzig 2003).

The baumhoferi *group*

In North America, 10 species are included in the *baumhoferi* group; only 2 of these species (*D. clarioralis* Walker and *D. pentictonella* Mutuura, Munroe and Ross) infest cones (Heinrich 1956; Mutuura *et al.* 1969; Neunzig 2003) (Table 1, Figs. 1, 3). *Dioryctria clarioralis* is distributed in the southeastern United States, whereas *D. pentictonella* occurs in the west and ranges from southern British Columbia to California and Nevada (Heinrich 1956; Mutuura *et al.* 1969; Neunzig 2003). Larvae of *D. clarioralis* are an economically important pest of seed orchards in the southern United States; *D. pentictonella* represents less of an economic issue.

The erythropasa *group*

Dioryctria erythropasa Dyar is the sole North American species in this group. Other species are recorded in Central and South America (Neunzig 2003) (Table 1).

The pygmaeella *group*

The two members of the *pygmaeella* group, *D. pygmaeella* Ragonot and *D. caesirufella* Blanchard and Knudson (Table 1, Fig. 3), are unique within *Dioryctria* as cone-feeders on Taxodiaceae (Merkel 1982; Neunzig 2003). *Dioryctria pygmaeella* is restricted to the coastal plains of the eastern United States and eastern Texas; *D. caesirufella* is known from east-central Texas and northeastern Mexico (Blanchard and Knudson 1983; Neunzig 2003).

The schuetzeella *group*

The *schuetzeella* group consists of *D. reniculelloides* Mutuura and Munroe and *D. pseudotsugella* Munroe (Table 1, Figs. 1, 3). *Dioryctria reniculelloides* is widely distributed throughout southern Canada and the northern United States; *D. pseudotsugella* is more limited in range, recorded in British Columbia and the northwestern United States. Roe and Sperling (2007) have addressed the diagnosis and delimitation of these two species.

The zimmermani *group*

The *zimmermani* group contains 18 species, 7 of which infest cones: *D. amatella* Hulst, *D. cambiicola* Dyar, *D. merkeli* Mutuura and Munroe, *D. resinosella* Mutuura, *D. taedae* Schaber and Wood, *D. taedivorella* Neunzig and Leidy, and *D. yatesi* Mutuura and Munroe (Table 1, Figs. 1, 3). Of these species, *D. amatella* and *D. merkeli* are the most pestiferous. As with the *abietella* group, taxonomic confusion within the *zimmermani* group is prevalent, owing to the lack of diagnostic features and overlap between larval hosts. Based on the degree of morphological and larval host overlap, an examination of the species limits among members of the *zimmermani* group is needed.

Dioryctria taedae is an important pest of loblolly pine, *Pinus taeda* L., initially associated with a range from Delaware to Georgia (Schaber and Wood 1971). This species has been routinely confused with the morphologically similar species *D. amatella* and *D. merkeli*. In fact, the type series for *D. taedae* contains both *D. merkeli* and *D. amatella* material, which adds to the confusion (Hedlin *et al.* 1980). *Dioryctria amatella* occurs in the southeastern United States (Neunzig *et al.* 1964; Neunzig 2003), and is sympatric with *D. taedae* in parts of its range. Although *D. amatella* is considered the primary pest of longleaf pine, *Pinus palustris* Miller, it is known to infest most other pines within its range, making the use of larval host as a diagnostic character for species in that region nearly impossible (Hedlin *et al.* 1980; Neunzig 2003). *Dioryctria taedivorella* Neunzig and Leidy ranges from eastern Virginia and North Carolina to northern Alabama and Mississippi (Neunzig and Leidy 1989; Neunzig 2003) and is also a pest of loblolly pine. In the past, this species has been confused with *D. merkeli* and *D. zimmermani* Grote, although the latter is now considered to be a cambial-tissue borer (Neunzig 2003). *Dioryctria merkeli* is morphologically similar to a number of other species throughout its range. The hosts for *D. merkeli* are slash, *Pinus elliottii* Engelmann, and longleaf pine in northern Florida, southern Georgia, and southern Mississippi (Mutuura and Munroe 1979). Although Mutuura and Munroe (1979) also included Virginia, Maryland, North Carolina, and eastern Texas as part of the range of *D. merkeli*, these occurrences likely pertain to other species (Neunzig 2003). *Dioryctria yatesi* is restricted to the mountains of the coastal southeastern United States and Tennessee and is the only member of the *zimmermani* group to infest table mountain pine, *Pinus pungens* Lambert (Mutuura and Munroe 1979; Neunzig 2003). *Dioryctria resinosella* Mutuura feeds on red pine, *Pinus resinosa* Aiton, which is found throughout southern Ontario and in the northeastern United States from Maine to Minnesota (Mutuura 1982; Neunzig 2003). *Dioryctria cambiicola* is the only known cone-infesting member of the *zimmermani* group in western North America. Mutuura *et al.* (1969) reported *D. cambiicola* throughout British Columbia and the western United States. *Dioryctria cambiicola* has been recorded only on lodgepole pine, *Pinus contorta* Douglas *ex* Loudon. The confusion that exists in the *zimmermani* group, coupled with its economic importance, makes a taxonomic revision of this group necessary.

Overall, *Dioryctria* taxa show a wide range of host associations and feeding habits within and between species groups (Table 1, Fig. 1). Host associations partially determine landscape-level distribution patterns; however, the mechanisms driving these patterns remain unexplored. In particular, distribution patterns of polyphagous *Dioryctria* are likely structured by host preferences that vary within and between geographic regions. Within geographic regions, the behaviours and interactions that mediate dispersal into appropriate habitats, and host-finding within such habitats, should be investigated. Information related to landscape-level distribution patterns will contribute to monitoring and prediction protocols that are required by integrated pest management programs (Fig. 4).

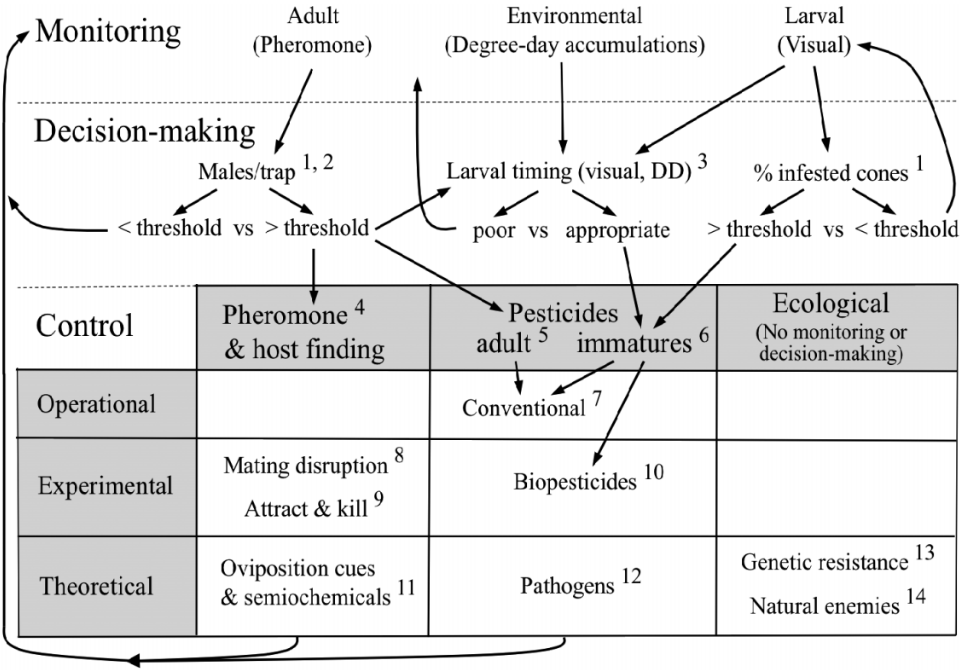
General biology

Research on the biology of seed-feeding *Dioryctria* species has been insufficient to facilitate the development of sophisticated integrated pest management programs for use in seed orchards. Identification of the processes driving spatial and temporal distributions of populations will provide the foundation for the development of management programs. This section explores the life history, reproductive traits, and host use of North American *Dioryctria* species and describes knowledge gaps that require further research.

Seasonal and diurnal phenology

Most *Dioryctria* species exhibit protandry on a seasonal basis. The initiation of seasonal activity by *Dioryctria* species varies with location, though activity commonly extends from early spring to early fall. Multivoltism exists in several

Fig. 4. Flow chart for managing *Dioryctria* species in conifer seed orchards. Results obtained from monitoring protocols (top portion) flow to inform decision-making methods (middle portion) and, subsequently, control strategies and tactics (bottom table). Control strategies are identified as operational (currently used in managed seed orchards), experimental (show promise and are under active investigation to bring to operational use), and theoretical (conceptually plausible, but not currently under investigation). The success of control actions is determined by a return to monitoring protocols. Numbers denote points needing further research to enable implementation: 1, determine economic or action thresholds for density/damage relationships, value of seed, and cost of controls; 2, quantify the relationship of male trap catches to female density, oviposition, and cone damage; determine the dispersal of mated and unmated females within and among areas; 3, create a day-degree model to predict moth development and time control efforts; 4, identify, produce, and commercialize pheromones; 5, determine rates of immigration and reinvasion, and the relationship between male trap catches and female densities; 6, determine the efficacy of ovicidal, long-residual, and systemic insecticides; 7, determine the efficacy of systemic and new, taxon-specific insecticides; 8, study the immigration/emigration of mated and unmated females, reproductive behaviour, and an abundant, inexpensive supply of pheromones; 9, study the immigration/emigration of mated and unmated females, reproductive behaviour, and use of expensive, less readily available pheromones; 10, determine the operational development of *Bacillus thuringiensis* Berliner subsp. *kurstaki* (Bacillaceae); 11, clarify the roles of visual, tactile, and semiochemical cues in host-finding and oviposition; 12, identify and culture host-specific viral and bacterial pathogens that could be applied in response to high moth densities; 13, determine clonal variation and heritability of *Dioryctria* susceptibility and the economics of breeding for resistance; 14, determine the incidence, taxonomic identity, geographic ranges, and efficacy of predators and parasitoids in controlling *Dioryctria* populations; study ecological modification in order to encourage natural enemies.



Control	Pheromone 4 & host finding	Pesticides adult 5 immatures 6	Ecological (No monitoring or decision-making)
Operational		Conventional 7	
Experimental	Mating disruption 8 Attract & kill 9	Biopesticides 10	
Theoretical	Oviposition cues & semiochemicals 11	Pathogens 12	Genetic resistance 13 Natural enemies 14

species especially those in warmer climates. Adult *Dioryctria* generally eclose at night and are active soon after dark (Fatzinger and Asher 1971*a*; Trudel *et al.* 1995). The phenology and location of oviposition and larval development are influenced by host biology. Although the majority of *Dioryctria* species pupate within or near the cone, pupation can also occur in the soil proximate to the host tree.

The abietella *group*

Populations of *D. abietivorella* are univoltine in the northern parts of its range (Hedlin *et al.* 1980) but bivoltine in the northwestern

United States (Keen 1952). Adult males are captured in pheromone-baited traps between May and October in the western provinces and states (Roe *et al.* 2006; unpublished data). It is unclear whether two periods of adult flight, in spring and late summer/fall (Hedlin *et al.* 1980), correspond to two distinct generations or to prolonged development of a single generation. Overlap between generations is supported by the presence of different larval instars in midsummer (Lyons 1957). Alternative developmental pathways may also occur: some *D. abietivorella* larvae develop through mid to late summer, whereas others enter diapause and overwinter (Lyons 1957). MacKay (1943) reports only one flight period, in June, throughout the species' range in Canada.

In contrast to *D. abietivorella*, *D. ebeli* exhibits five or six generations per year in northern Florida (Ebel 1965). Multivoltism of *D. ebeli* is facilitated by moderate winter temperatures and larval use of seasonally available tissues (Ebel 1965). Rust-infected cones are essential habitat for *D. ebeli* in late fall and spring, while second-year cones of slash pine are readily infested in summer and early fall (Ebel 1965).

Flight of male *D. abietivorella* in response to sex pheromone begins 2 h after sunset, peaks 4 h after sunset, and ends 1 h after dawn (unpublished data). Oviposition by *D. abietivorella* typically begins the night following mating, and can continue for up to 2 weeks (Trudel *et al.* 1995). Eggs are laid singly or in small clusters on or between cone scales and on needles (Lyons 1957; Ruth 1980; Martineau 1984). Female *D. abietivorella* lay a maximum of 100 eggs and an average of 25 eggs throughout their lifetime (Trudel *et al.* 1995), and are less fecund than female *D. ebeli*, which lay upwards of 300 eggs (Ebel 1965). *Dioryctria ebeli* oviposit for approximately 1 week on substrates that include male flower scales and rust-infected cones (Ebel 1965).

Eggs of *D. abietivorella* are approximately 1 mm in diameter, oval, and flattened, with a stellate pattern of ridges on the chorionated surface (Lyons 1957; Ebel 1965) (Fig. 2). Like those of other *Dioryctria* species (McLeod and Daviault 1963; Ebel 1965; Pasek and Dix 1989), newly laid *D. abietivorella* eggs are creamy white and turn reddish as development progresses (unpublished data). The dark head capsule of the embryo is discernible through the chorion prior to egg hatch (McLeod and Daviault 1963; Pasek and Dix 1989), which occurs approximately 7 days after oviposition at 25 °C for *D. abietivorella* (unpublished data) and in 3–4 days at 27 °C for *D. ebeli* (Ebel 1965). At 25 °C, with a 16L:8D light cycle, *D. abietivorella* larvae develop through five (occasionally six) instars within 23 days (Trudel *et al.* 1995). Once feeding is complete, *D. abietivorella* larvae exit the cone to pupate inside a frass-covered cocoon (Keen 1952; Lyons 1957; Trudel *et al.* 1999*a*). Pupation may occur in the duff (Keen 1952; Ebel 1965; Martineau 1984; Trudel *et al.* 1999*a*) or in a frass webbing on the exterior of the cone (Keen 1952). *Dioryctria ebeli* also leave the cone to pupate, and adult eclosion occurs in 11 days at 24 °C (Ebel 1965; Neunzig and Merkel 1967).

The **auranticella** *group*

Members of the *auranticella* group are typically univoltine (Neunzig *et al.* 1964; Pasek and Dix 1989). Studies conducted in North Carolina and Ontario report one generation of *D. disclusa*, with adult flight in early summer in the south (Neunzig *et al.* 1964; Pasek and Dix 1989) and midsummer in the north (Lyons 1957). *Dioryctria disclusa* overwinter as early-instar larvae in Ontario beneath bark scales of red pine (Lyons 1957) but as late instars in cones in the southern parts of its range (Neunzig *et al.* 1964). *Dioryctria auranticella* is similarly univoltine, with peak adult flight occurring in midsummer (Pasek and Dix 1989).

Information on oviposition and fecundity of *Dioryctria* species in the *auranticella* group is limited. Male *D. auranticella* (Pasek and Dix 1989) and *D. disclusa* (Lyons 1957) emerge 2 or 3 and 5 days before females, respectively. One female *D. auranticella* reportedly laid 27 eggs in her lifetime (Pasek and Dix 1989); female *D. disclusa* lay, on average, 10–55 eggs, but can produce over 100 in their lifetime (Lyons 1957). *Dioryctria disclusa* eggs are laid under the bark scales of needle-free portions of red pine branches (Lyons 1957). *Dioryctria auranticella* eggs require an incubation period of 6–9 days at 26 ± 2 °C (Pasek and Dix 1989). Larvae of both species feed on staminate flowers in early spring and then disperse to second-year cones later in the season. *Dioryctria auranticella* pupate inside the cone and eclose after 15 days when held at 23 °C (Pasek and Dix 1989). *Dioryctria disclusa* also pupate inside or on the cone (Farrier and Tauber 1953; Neunzig and Merkel 1967).

The baumhoferi *group*

Information regarding the phenology of the *baumhoferi* group is limited to *D. clarioralis*, which is generally univoltine (Neunzig *et al.* 1964) but may be multivoltine in the southern reaches of its range (Yates and Ebel 1975). In Florida, larvae infest buds and first-year cones between November and April (Ebel 1965). Infestations in second-year cones occur in late winter and spring, and pupae are found in early spring (Ebel 1965). Pupae occur on trees or in the soil and eclose in about 14 days when held at 24 °C (Neunzig *et al.* 1964; Ebel 1965).

The pygmaeella *group*

Dioryctria pygmaeella is multivoltine and can complete up to three generations per year (Merkel 1982). Eggs are laid in niches between cone scales close to the basal region of the cone. Eggs hatch within a week; neonates eat the chorion and bore into the cone after making exploratory holes (Merkel 1982). Larval development is complete within 25 days and pupation occurs in the cone. Exit holes are created prior to pupation and are closed with a thin, paperlike cover through which adults eclose in approximately 2 weeks (Merkel 1982).

The schuetzeella *group*

Most of the phenological information for this group concerns *D. reniculelloides*, which is univoltine (MacKay 1943; McLeod and Daviault 1963). Caged females lay, on average, only nine eggs. Oviposition occurs in late summer in various protected locations, including niches on stem bark, on lichen, between cone scales, or within frass on damaged foliage (McLeod and Daviault 1963). Eggs hatch in 1 day under field conditions; early-instar larvae enter diapause without feeding (MacKay 1943; McLeod and Daviault 1963; Mutuura and Munroe 1973). Larvae are facultative cone-feeders that migrate between host tissues during development. In midspring, larvae feed on needles until cones become available (McLeod and Daviault 1963). Pupae are present in midsummer and adults fly in late summer (MacKay 1943; McLeod and Daviault 1963; Mutuura and Munroe 1973).

Dioryctria pseudotsugella larvae are present in late May to late June and adults occur in early July (Prentice 1965).

The zimmermani *group*

The phenology of members of the *zimmermani* group has been best studied in *D. amatella*. Voltinism varies between one and four generations per year in Florida (Ebel 1965); multivoltism is usual in Georgia and North Carolina (Coulson and Franklin 1970*b*). Adult flight occurs in spring and early fall, with less activity in midsummer (Neunzig *et al.* 1964; Coulson and Franklin 1970*b*; Yates and Ebel 1975; Hanula *et al.* 1985). Female *D. amatella* oviposit next to or directly on the larval substrate: second-year cones in the summer and fusiform rust cankers (*Cronartium* Fr.) in the fall (Coulson and Franklin 1970*a*, 1970*b*). Most eggs are laid 3–12 days after adult emergence, with peak oviposition occurring between days 5 and 7 (Hanula *et al.* 1984*b*). Oviposition can continue for up to 23 days (Hanula *et al.* 1984*b*) and lifetime fecundity can be as high as 300 eggs per female (Ebel 1965). *Dioryctria amatella* eggs held at 24 °C hatch in about 7 days (Ebel 1965). Egg-surface patterns in *D. amatella* are similar to those in *D. abietivorella*: radially symmetric ridges that are sinuous in *D. abietivorella* and straight in *D. amatella* (Ebel 1965).

Until pupation in early summer, *D. amatella* larvae develop in various tissues, including fusiform rust cankers, wounds, and second-year cones (Ebel 1965; Coulson and Franklin 1970*a*, 1970*b*). Some adults eclose in midsummer, while a portion of larvae undergo summer aestivation followed by adult eclosion in the fall. Midsummer adults oviposit to begin a second generation, with adult eclosion in November. Second-generation adults lay eggs primarily in fusiform cankers or tree wounds; the resulting larvae feed through the winter

(Coulson and Franklin 1970*a*, 1970*b*). Some larvae also overwinter at the base of first-year cones, under unexpanded terminal needles, and in damaged second-year cones (Neunzig *et al.* 1964). In North Carolina, most *D. amatella* overwinter as early-instar larvae, although older larvae also overwinter (Neunzig *et al.* 1964). Development recommences in the spring and most adults emerge in early summer, when second-year cones serve as suitable oviposition sites. In some cases, adult eclosion occurs earlier in the spring and females must oviposit on other tissues such as branch terminals or first-year cones. The resulting larvae must migrate to second-year cones later in the season to complete development (Coulson and Franklin 1970*b*).

In conclusion, the development of pest-management programs depends on knowledge of phenology and how it is affected by environmental conditions and host interactions. Assessment of temperature thresholds for development, and determination of the influence of photoperiod and host phenology on development and mortality, are required in order to create management protocols. High-quality microhabitats for oviposition and larval feeding need to be identified to increase our understanding of local-scale distribution patterns. Furthermore, the effect of nutrition (larval, adult, and spermatophore-derived) on development and mortality rates should be measured. *Dioryctria* species display a wide range of overwintering habits, likely defined in part by host-tree phenology as well as latitude. Research on overwintering ecology is needed to pinpoint overwintering locations and life stages of pestiferous *Dioryctria* species. This information can be used to assess the need for control techniques and timing of their use. Identification of environmental cues that influence the phenology of *Dioryctria* will increase understanding of interspecies interactions, population dynamics, and the temporal distributions of various life stages. We also predict that within-species differences in seasonal activity along geographic gradients and with different host associations will be found; this information is necessary for site-specific management.

Reproductive biology

Detailed accounts of reproductive behaviour in some *Dioryctria* species are available (Fatzinger and Asher 1971*b*; Phelan and Baker 1990). In particular, the mating behaviour of *D. ebeli* (*abietella* group) and *D. amatella* (*zimmermani* group) have been thoroughly described (Fatzinger and Asher 1971*b*; Phelan and Baker 1990). Intraspecies differences in calling behaviour as well as in mating frequency exist. Recent advances have greatly expanded our understanding of sex-pheromone composition and intraspecific geographic variation in sex pheromones.

Delayed mating after adult eclosion seems to be prevalent in *Dioryctria* species. Mating behaviour begins 3–4, 2–3, and 2 days post eclosion in *D. abietivorella* (Trudel *et al.* 1995), *D. amatella* (Ebel 1965; Fatzinger 1981; Hanula *et al.* 1984*b*), and *D. auranticella* (Pasek and Dix 1989), respectively. At least in *D. abietivorella*, this delay in mating may correlate with egg maturation (unpublished data).

Dioryctria species exhibit polyandrous mating patterns in seed orchards. In southern British Columbia, females in the *auranticella*, *abietella*, *ponderosae*, and *zimmermani* groups mate multiple times throughout the season (unpublished data). This behaviour occurs in stands of Douglas-fir, *Pseudotsuga menziesii*, (Mirb.) Franco (Pinaceae), lodgepole pine, *Pinus contorta*, and a spruce hybrid complex collectively termed "interior spruce" (Pinaceae) (Coates, D.K. 1994). Preliminary data indicate that individuals of *D. abietivorella* mate up to eight times; those of other species mate just two or three times (unpublished data). Interspecific differences in benefits accrued by females through multiple matings may explain the differences in mating frequency. It is not known whether male investment is important to female fitness and receptivity in *Dioryctria*. The effect of male investment may be species-specific, which could cause mating frequency to vary among species.

As with other moths, mate-finding in *Dioryctria* is mediated by female-produced sex pheromones. For many species groups, females' pheromone production and release behaviour (calling) have not been described. Calling behaviour of females in the *abietella* group in

North America is known only for *D. ebeli.* Virgin females initiate calling 5−6 h after the onset of scotophase under a 12L:12D cycle; calling peaks 9 h after dark and stops before the onset of photophase (Fatzinger and Asher 1971*b*). Females assume a characteristic calling position with the tip of the abdomen curved upwards between the wings and the pheromone gland extruded from the tip of the ovipositor (Fatzinger and Asher 1971*b*). At 1 day post eclosion, approximately 30% of *D. ebeli* call and are receptive to mating; the number of calling females doubles during the following scotophase (Fatzinger and Asher 1971*b*). Female *D. disclusa* (*auranticella* group) begin calling 3−5 h after sunset, and male moth flight to pheromone follows the same periodicity (DeBarr and Berisford 1981).

The female-produced sex pheromones of nine *Dioryctria* species are known (Table 3) and synthetic-pheromone-baited traps are used to monitor adult activity of various species in seed orchards (Hanula *et al.* 1984*a*, 1984*c*; Hanula *et al.* 2002; Strong *et al.* 2008). For six of the nine species, *Z*9-tetradecenyl acetate (*Z*9–14:Ac) is the major component, although the importance of this component for *D. abietivorella* varies geographically (Grant *et al.* 2009).

The sex pheromone of *D. abietivorella* contains two major components, (*Z*9, *E*11)-tetradecadienyl acetate (*Z*9, *E*11–14:Ac) and (*Z*3, *Z*6, *Z*9, *Z*12, *Z*15)-pentacosapentaene (C_{25} pentaene), neither of which is typically found in the sex pheromone gland extracts of other *Dioryctria* species (Millar *et al.* 2005) (Table 3). C_{25} pentaene only weakly stimulates male moth antennae in electroantennographic assays but the addition of this component is crucial for attracting males in field trials in western North America. A third component, *Z*9-tetradecenyl acetate (*Z*9–14:Ac), occurs in small amounts in female gland extracts (Millar *et al.* 2005). Because these pheromone components have different vapour pressures and belong to different structural classes, it is likely that they are produced through independent biosynthetic pathways (Millar *et al.* 2005); how females emit the precise ratios of the two components is not known. A 1:10 ratio of synthetic *Z*9, *E*11–14:Ac to C_{25} pentaene attracts male *D. abietivorella* in field trials (Table 3) but does not reflect the ratio of components stored in the female pheromone gland (Strong *et al.* 2008).

The response of male *D. abietivorella* to female sex pheromones varies geographically (Table 3), which may indicate the presence of different pheromone races (Grant *et al.* 2009). Lures loaded with a 1:10 ratio of *Z*9, *E*11–14:Ac to C_{25} pentaene are attractive to males in western (Strong *et al.* 2008) but not eastern Canada (Grant *et al.* 2009). In eastern populations, the addition of *Z*9–14:Ac is crucial to elicit male response (Grant *et al.* 2009). Male response to pheromones should be assessed in the populations located in the intervening geographic regions. Geographic variation of pheromone production throughout the large range of this species should be examined also. The minor pheromone component identified in *D. abietivorella* pheromone gland extracts, *Z*9–14:Ac, does not occur in its close European relative, *D. abietella* (Löfstedt *et al.* 1983), or in *D. ebeli* (Miller *et al.* 2010) (Table 3), the other North American member of the *abietella* group.

Female *D. ebeli* produce *Z*9, *E*11–14:Ac, a component of the *D. abietivorella* sex pheromone. Male *D. ebeli* are responsive to synthetic lures combining *Z*9, *E*11–14:Ac and C_{25} pentaene, the second crucial component of female *D. abietivorella* sex pheromone (Miller *et al.* 2010) (Table 3). Additional work is required to determine whether other pheromone components, such as C_{25} pentaene, are produced by female *D. ebeli* (Miller *et al.* 2010).

Limited information on pheromone biology is available for other species groups. Field trials that tested the attractiveness of C_{25} pentaene combined with the previously identified sex-pheromone components of *D. amatella* (*zimmermani* group) and *D. disclusa* (*auranticella* group) show an increase in male response in both species. Increased male response was not seen in similar studies targeting *D. merkeli* (*zimmermani* group) (Miller *et al.* 2010). *Dioryctria resinosella* (*zimmermani* group) requires a four-component blend that includes an alcohol, unique within this genus (Grant *et al.* 1993). The most attractive blend for *D. resinosella* contains *Z*9-tetradecen-1-ol (Z9–14:OH) and *Z*9-dodecenyl acetate (Z9–12:Ac), although the latter component has not been found in female gland extracts (Grant *et al.* 1993).

Table 3. Sex-pheromone blends for North American cone-feeding *Dioryctria* species (modified from Pherolist (www.nysaes.cornell.edu/pheronet/) and updated to include current research).

	Component(s)	Female-produced blend*	Blend attractive to males (μg)†	Reference
***abietella* group**				
D. abietivorella (eastern)	(*Z*)-9-tetradecenyl acetate* (9*Z*,11*E*)-tetradecadienyl acetate* (3*Z*,6*Z*,9*Z*,12*Z*,15*Z*)-pentacosapentaene*	1:4:10	67:200:2000	Millar *et al*. 2005; Strong *et al*. 2008; Grant *et al*. 2009
D. abietivorella (western)	(*Z*)-9-tetradecenyl acetate*‡ (9*Z*,11*E*)-tetradecadienyl acetate* (3*Z*,6*Z*,9*Z*,12*Z*,15*Z*)-pentacosapentaene*	1:1	200:2000	Millar *et al*. 2005; Strong *et al*. 2008
D. ebeli	(9*Z*,11*E*)-tetradecadienyl acetate* (3*Z*,6*Z*,9*Z*,12*Z*,15*Z*)-pentacosapentaene	0.51–1.58 ng	1:10	Millar *et al*. 2010
***auranticella* group**				
D. auranticella	*Z*9-tetradecenyl acetate*	Not reported		Pasek and Dix 1989
D. disclusa	*Z*9-tetradecenyl acetate* (3*Z*,6*Z*,9*Z*,12*Z*,15*Z*)-pentacosapentaene		30–300 1:10	Meyer *et al*. 1982; Hanula *et al*. 1984*a*; Miller *et al*. 2010
***baumhoferi* group**				
D. clarioralis	*Z*9-tetradecenyl acetate* *E*9-tetradecenyl acetate* *Z*11-hexadecenyl acetate	12:88	30:3.6:1.5–3	Hanula *et al*. 1984*a*; Meyer *et al*. 1984
***schuetzeella* group**				
D. reniculelloides	*Z*9-tetradecenyl acetate* *Z*7- dodecenyl acetate *Z*7-dococenal		3:0.15 3:0.15:0.15	Grant *et al*. 1987
***zimmermani* group**				
D. amatella	*Z*11-hexadecenyl acetate* (3*Z*,6*Z*,9*Z*,12*Z*,15*Z*)-pentacosapentaene		100 1:10	Hanula *et al*. 1984*a*; Meyer *et al*. 1986; Miller *et al*. 2010
D. merkeli	*Z*9-tetradecenyl acetate *E*9-tetradecenyl acetate		30:0–4.5	Meyer *et al*. 1984; Hanula *et al*. 1984*a*

Table 3 (*concluded*).

	Component(s)	Female-produced blend*	Blend attractive to males (µg)†	Reference
D. resinosella	*Z*9-tetradecenyl acetate* *Z*9-tetradecen-1-ol* *Z*9- dodecenyl acetate *E*9-tetradecenyl acetate	1:0.2	30:5:10:1.5	Grant *et al.* 1993

*Detected in female sex pheromone gland extracts.
†Amount (µg) loaded on rubber-septum lures.
‡This component is not attractive to males in field trials.

Only one pheromone component, *Z*9–14:Ac, has been identified in female gland extracts of *D. reniculelloides* (*schuetzeella* group) (Grant *et al.* 1987). In electroantennogram assays of male *D. reniculelloides*, antennal responses were elicited by *Z*9–14:Ac, *Z*7-dodecenyl acetate (*Z*7–12:Ac), and *Z*7-dodecenal (*Z*7–12:Ald). The blend most attractive to male *D. reniculelloides* in field assays contained *Z*9–14:Ac as the major component and *Z*7–12:Ac or *Z*7–12:Ac and *Z*7–12:Ald as minor components (Grant *et al.* 1987). *Dioryctria reniculelloides* is sympatric with *D. abietivorella*, utilizes many of the same hosts (Neunzig 2003), and has overlapping adult flight activity. Interspecific differences in pheromone blends may be a mechanism to reduce competition in pheromone communication (Evenden *et al.* 1999).

There is great potential for the use of synthetic sex pheromones to control pestiferous *Dioryctria* species. Seed orchards provide suitable conditions for the application of mating disruption or attract-and-kill formulations that have been widely adopted in fruit orchards (Witzgall *et al.* 2008). Future research should address the stability of pheromone components under field conditions and determine whether the full pheromone blend is required in order to disrupt mating behaviour. The identity of the sex pheromones of various *Dioryctria* species may serve as a useful trait to include in phylogenetic analyses of this taxonomically difficult group.

Host use: semiochemicals and larval feeding

Semiochemicals are important cues that mediate host use by females of *Dioryctria* species, although information beyond basic identification of host cues is limited. Landscape-level distributions could be driven in part by host-cue-mediated migration. Pheromone trapping studies indicate that traps placed higher in the canopy (where the highest density of cones and the majority of females occur) capture more male moths than do lower-placed traps (Hanula *et al.* 1984*c*; Strong *et al.* 2008). The local-scale distribution of females and males may be influenced by cone-derived host cues; the distribution of males is also likely mediated through the presence of females.

Oviposition

The monoterpenes myrcene and car-3-ene, released from twigs of eastern white pine, *Pinus strobus* L., elicit both antennal and oviposition responses from female *D. abietivorella* (Shu *et al.* 1997). Although (−)-limonene is another oviposition stimulant, it does not trigger significant electrophysiological responses from antennae (Shu *et al.* 1997). These monoterpenes stimulate greater antennal responses from older, mated females than from younger virgins. Increased antennal responsiveness is correlated with increased oviposition, although whether host volatiles actually attract gravid females to oviposition sites is not known (Shu *et al.* 1997). Adult male and female *D. ebeli* show greater antennal responses to volatiles emitted from the basal and stalk portion of first-year cones of slash pine than to second-year cones or the apical and middle portions of first-year cones, indicating that the basal cone region may be an important oviposition site (Asher 1970).

In the laboratory, female *D. amatella* (*zimmermani* group) will initiate calling, mating, and oviposition only in the presence of fusiform rust galls (Fatzinger 1981). *Dioryctria amatella* females use α-pinene as an oviposition stimulant; female response is increased by the presence of myrcene and limonene (Hanula *et al.* 1985). Female *D. amatella* prefer oviposition substrates with high monoterpene content even though feeding by first-instar larvae is negatively correlated with monoterpene content.

Host acceptance and oviposition in various species of *Dioryctria* appear to be influenced by host monoterpene emissions; these behaviours could be exploited for pest-management purposes. Future research should identify cues used by females for host recognition and acceptance. Migration may also be mediated through host cues; this is another tactic that could be used to deter pest populations.

Larval feeding

Larval feeding on cones reduces the reproductive potential of the tree host. In some *Dioryctria* species, larvae migrate between cones as resources are depleted, thus damaging multiple cones during their development (Lyons 1957; Neunzig 2003). In addition, larvae can use entry holes created by other insects and thereby act as secondary pests that amplify primary damage (Heinrich 1956; Lyons 1957; Ruth 1980; Fidgen and Sweeney 1996).

Infestations by larval *D. abietivorella* can be detected from an external accumulation of frass, without pitch secretions, on the cone (Fig. 2) (Keen 1952; Lyons 1957; Ross and Evans 1957; Hedlin *et al.* 1980; Ruth 1980). In addition to cones, *D. abietivorella* larvae feed on other host tissues including needles, shoots, twigs, and cambial tissue of the tree bole (*e.g.*, wound tissue, galls, and graft unions) (Hedlin *et al.* 1980; Ruth 1980). These other tissues appear to provide suboptimal nutrition or greater exposure to natural enemies because larvae feeding on foliage and bark incur higher mortality than those feeding on cones (Trudel *et al* 1999*b*).

Although some *Dioryctria* species are polyphagous, larval performance on the various hosts is unequal. Field-reared *D. abietivorella* larvae have different survival rates when reared on white spruce, black spruce, *Picea mariana* (Miller) Britton, Sterns and Poggenb. (Pinaceae), and jack pine, *Pinus banksiana* Lambert (Trudel *et al.* 1999*b*). Larvae reared on white spruce, black spruce, and jack pine show the highest, intermediate, and poorest survival rates, respectively. Larval development times on white and black spruce are similar, but development is prolonged on jack pine. These differences in larval performance on different hosts likely contribute to a host-preference hierarchy that should be identified for monitoring purposes.

In the *zimmermani* group, *D. amatella* larvae feed on different tissue types at different times during the season. In late summer, up to seven different larval stadia can be found feeding in the same cone (Hanula *et al.* 1985). At the beginning of the season, *D. auranticella* larvae feed on male and female flowers and then migrate to second-year cones. Larvae often require two cones to complete development (Pasek and Dix 1989). Larvae of *D. disclusa* (*auranticella* group) also damage multiple cones during development (Neunzig *et al.* 1964).

Host-preference hierarchies in polyphagous species of *Dioryctria* remain unexplored, but may govern landscape-level population distributions. Local-scale larval-distribution patterns are likely mediated by feeding stimulants and deterrents as well as by inter- and intra-specific competition. It is unclear how larval nutrition influences adult fitness, particularly when larvae feed on a less favourable host or tissue type.

Evolutionary ecology

Fluctuating abundance of food resources

Temporal heterogeneity in food resources has likely been a strong driving force in the evolution of *Dioryctria*. Monophagous species of *Dioryctria* (*e.g.*, feed on one conifer genus), such as *D. ebeli* (Table 1, Fig. 1), are not typically associated with economically damaging levels of infestation. This situation contrasts with polyphagous members of the *abietella* group, *D. abietivorella* and *D. abietella*, which are significant pests. Host-switching by polyphagous species may allow high population densities to be maintained despite temporal heterogeneity in the availability of cone crops (Janzen 1971). The causal mechanisms linking polyphagy and pest status require further clarification. Despite its monophagous lifestyle, *D. amatella* (*zimmermani* group) is a serious pest of pines, developing on a variety of host tissues, which permits year-round development and reproduction (Coulson and Franklin 1970*b*). Continued development during the winter may give *D. amatella* a competitive advantage. This plasticity in tissue use may sustain high population densities in years when cone crops are poor.

Sympatry and interspecific competition

One way in which sympatric species reduce interspecific competition is through resource partitioning and utilization (Grinnell 1924). This strategy may be another factor in the evolution of the patterns of tissue use and host association of sympatric *Dioryctria* species (Table 1, Fig. 1). Members of the *pygmaeella* group are sympatric with some *baumhoferi*-group species and with *D. amatella* (*zimmermani* group) (Table 1). *Pygmaeella*-group species utilize members of Cupressaceae rather than Pinaceae, while *baumhoferi*-group and *zimmermani*-group species feed solely on *Pinus*. Use of *Taxodium* by members of the *pygmaeella* group may permit sympatry of these species. Little genetic information about the *pygmaeella* group is available; its relatedness to the *baumhoferi* and *zimmermani* groups is not known.

Dioryctria abietivorella and members of the *schuetzeella* group overlap in geographic range and host associations but differ in host-tissue use. *Dioryctria abietivorella* are primarily cone-feeders; *schuetzeella*-group species are predominantly foliage-feeders. Similarly, the closely related sympatric species *D. cambiicola* and *D. abietivorella* both feed on lodgepole pine, but *D. cambiicola* feeds primarily on cambium, whereas *D. abietivorella* favours cones. Differential tissue use also occurs in sympatric *ponderosae*-group species feeding on ponderosa pine: *D. auranticella* feeds primarily on cones, the others specialize on healthy and rust-infected cambium.

Between-season differences in tissue use by *Dioryctria* species in the southeastern United States may also facilitate sympatry. A survey of *Dioryctria* species infesting slash and longleaf pine in northern Florida highlighted the differences in tissue use between tree hosts and throughout the season (Ebel 1965). Although *D. amatella, D. clarioralis, and D. ebeli* occur on both pine species, *D. amatella* and *D. ebeli* are most abundant on slash pine, whereas *D. clarioralis* are more commonly found on longleaf pine. On slash pine, the majority of *D. amatella* occur in fusiform cankers, *D. ebeli* on cones with rust, and *D. clarioralis* on male strobili. On longleaf pine, *D. amatella* and *D. ebeli* are most commonly found in healthy second-year cones, whereas *D. clarioralis* occurs primarily in first-year cones. Spring populations of *D. amatella* larvae are frequently found in male and female flower buds, new shoots, overwintering cones, and fusiform rust cankers. Later in the spring, rust-infected cones are also infested by *D. amatella*. In spring, *D. ebeli* can be found on first-year cones and vegetative buds as well as on second-year longleaf pine cones. During the summer, *D. amatella* larvae generally feed on second-year cones, whereas *D. ebeli* larvae are abundant in second-year slash pine cones. In the fall and winter, *D. amatella* larvae are again located on bud scales, cone stalks, and cankers of longleaf pine. Fall populations of *D. ebeli* larvae frequently infest second-year longleaf pine cones and overwinter on buds or cankers, which is similar to *D. amatella*. Year-round, *D. clarioralis* larvae feed on buds and young cones. *Dioryctria ebeli* larvae feed on tissue with less resin than do *D. amatella* larvae and will often remain within the same tissue to complete development. As well, *D. ebeli* often infest material damaged by *D. amatella*. Although causal mechanisms are unknown, resource partitioning by *Dioryctria* may allow sympatric species to coexist.

Pest status and management

Infestations of seed-feeding *Dioryctria* species can have a significant economic impact on production of seed used for conifer propagation. Although infestations are most detrimental in seed orchards, natural stands can also be affected. Knowledge of the life history and distribution patterns of *Dioryctria* species in both managed and natural stands will provide the framework for developing effective pest-monitoring and -management techniques (Table 4, Fig. 4). This section describes the pest status, monitoring, and control of seed-feeding *Dioryctria* species considered to be pests, and identifies where further research should be directed.

Impacts in natural forest stands

Little documentation is available on rates of infestation by North American *Dioryctria* species in natural forest stands. In the western United States, cones of whitebark pine, *Pinus albicaulis* Engelmann, suffer up to 68% infestation by *D. abietivorella*, with 13% seed loss (Kegley *et al.* 2001). Cones in wild stands of Douglas-fir and hemlock, *Tsuga* Carrière (Pinaceae), are subject to attack by *Dioryctria* species in western North America (Furniss and Carolin 1977).

Dioryctria abietella, a European member of the *abietella* group, infests cones of at least nine conifer species (Roques 1983; Lee and Lee 1994), destroying cones, consuming seeds, and reducing germination of Bhutan pine, *Pinus wallichiana* A.B. Jacks (Bhandari *et al.* 2006*b*). In Switzerland, *D. abietella* infestations damage up to 33% of cones of Swiss stone pine, *Pinus cembra* L. (Dormont and Roques 1999), and 8% of cones of Norway spruce, *Picea abies* (L.) Karst., with 29% seed loss per infested cone (Seifert *et al.* 2000). Fourteen percent of cones of European silver fir, *Abies alba* Mill. (Pinaceae), in Poland were infested by *D. abietella* (Skrzypczyńska 2004).

In natural stands, temporal heterogeneity of food sources is an important factor that regulates populations of seed-feeding *Dioryctria* species (Turgeon *et al.* 1994). Mast-seeding occurs in many conifer genera and may have evolved as a tactic to avoid severe seed herbivory (Janzen 1971; Silvertown 1980; Kelly 1994). Mast-seeding results in highly variable seed crops between years but synchronous seed production within a year (Silvertown 1980; Kelly 1994). During mast years, trees produce abundant seed-cone crops that satiate herbivores, allowing a proportion of the seed to escape herbivory. The length of time between mast years is variable; cone yields can be very low during the intervening period (Silvertown 1980). In the year following a mast-seeding event, herbivore population densities increase in response to the previous year's abundant food sources (Hedlin 1974; Miller *et al.* 1984) but then decline between mast years (Miller *et al.* 1984; Shea 1989). As a result, the episodic nature of cone production may prevent the establishment of large, stable populations of specialist seed-feeders. Polyphagous species such as *D. abietivorella* can feed on alternative tissues and host species between mast crops. Seed-feeders can also respond to heterogeneity in cone crops either spatially by moth dispersal (Mosseler *et al.* 1992) or temporally through prolonged larval diapause (Turgeon *et al.* 1994).

Seed-feeders may severely reduce the reproductive success of rare conifer species (Mosseler *et al.* 1992). In Newfoundland in 1988, a large, geographic-scale masting event occurred in black spruce, white spruce, eastern tamarack, *Larix laricina* (Du Roi) Koch (Pinaceae), and balsam fir, *Abies balsamea* (L.) Miller, followed by a rare 3-year mast-seeding event in red pine (Mosseler *et al.* 1992). The consistently large red pine cone crops, coupled with low cone crops in other conifers, may have served to concentrate the polyphagous *D. abietivorella* on the rarely exploited red pine. Cone infestation ranged from 8% in lightly infested stands to 98% in highly infested stands. The number of full seeds in severely infested trees was reduced

Table 4. Gaps in knowledge of the biology and ecology of *Dioryctria* species and pest-management applications that could be developed if missing information is obtained.

	Egg	Larva	Pupa	Adult	Application
Distribution					
Large scale[a]	Edge effects Important habitat traits	Movement between trees Masting events	Soil composition Meteorological effect on survival	Migration Habitat finding	Habitat management Monitoring techniques
Small scale[b]	Oviposition stimulants/deterrents Effect of density on oviposition	Feeding stimulants/deterrent Predation and competition effects	Predation rates	Predation, competition Synergy of semiochemicals and pheromones Dispersal (*e.g.*, pre/post mating, density effects)	Monitoring techniques Semiochemical-based trapping (monitoring, disruption) Feeding deterrents Predation enhancement
Temporal	Development thresholds Influence of photoperiod Host phenology Dayegree accumulations	Development thresholds Photoperiod influence (overwintering) Host phenology Day-degree accumulations	Influence of photoperiod	Temperature thresholds for flight/reproduction	Monitoring Timing of biopesticide or insecticide applications
Nutrition	Influence of female diet/spermatophore	Performance on secondary host species / tissue type Cannibalism and predation rates	Size effects on fitness	Nectar source Iinfluence of spermatophore	Kairomone-based attraction and killing
Natural enemies	Identity and mortality levels	Predators, parasites, and diseases Mortality rates	Predators and diseases Mortality rates	Predators	Biocontrol agents
Phenological and genetic diversity	Pesticide resistance Genetic diversity	Pesticide resistance Host races (as related to dispersal distance and gene flow) Genetic diversity Relationship to habitat heterogeneity	Pesticide resistance Genetic diversity	Geographic pheromone races Host races (as related to dispersal distance and gene flow) Genetic diversity Pesticide resistance Relationship to habitat heterogeneity	Identification for species- and host-race-specific monitoring and control strategies

[a] Landscape to tree.
[b] On tree.

by 93% compared with 11% in lightly infested trees. Large seed losses 2 years in a row can have a negative impact on the reproductive capacity of rare, patchily distributed conifer populations (Mosseler *et al.* 1992).

Impacts in conifer seed orchards

In managed forest systems, *Dioryctria* species are most problematic in conifer seed orchards that produce seed for reforestation programs (Pasek and Dix 1989; Schowalter 1994). Orchards are managed to increase seed quality and quantity as well as to decrease cone-crop variability between years (Zobel and Talbert 1984; Turgeon *et al.* 1994). Because seed orchards are monocultures and management practices attempt to circumvent mast-seeding, seed orchards provide an abundant and consistent food supply for seed-feeders, including *Dioryctria* species (Zobel and Talbert 1984; Turgeon *et al.* 1994).

Most conifer genera grown in seed orchards are subject to attack by *Dioryctria* species, with the notable exception of *Thuja* L. (Cupressaceae). Historically, up to 15.6% of seeds in Douglas-fir seed orchards in the western United States has been lost to *D. abietivorella* damage (Schowalter *et al.* 1985). Rates of *D. abietivorella* infestation as high as 42% occur in Idaho orchards of western white pine, *Pinus monticola* Douglas *ex* D. Don (Shea *et al.* 1986). Many Pinaceae species grown in seed orchards in Canada, including pines, spruces (*Picea* A. Dietr.), firs (*Abies* Mill.), larch (*Larix* Mill.), and Douglas-fir, incur seed-production losses caused by several species of *Dioryctria* (Turgeon and de Groot 1994; Turgeon *et al.* 2005). Up to 80% of cones were attacked in some spruce and Douglas-fir seed orchards in central British Columbia in 2004 (Strong 2005). Norway spruce seed orchards in Sweden are attacked by *D. abietella* larvae, with infestation rates between 23% and 77% (Rosenberg and Weslien 2005).

Seed pests cause direct and indirect damage to cone and seed production. Larval feeding results in smaller cones and lowered seed production per cone (Mosseler *et al.* 1992). Additionally, pathogens and phytophagous cone insects can promote the occurrence of secondary pests such as mycophages and saprophages, as well as other phytophages, and thereby amplify primary-cone damage (Turgeon *et al.* 1994). In black spruce and white spruce seed orchards, *D. abietivorella* infestation rates are higher on cones damaged by cone maggots, *Strobilomyia* Michelson (Diptera: Anthomyiidae), than on undamaged cones (Fidgen and Sweeney 1996). Preference for cones infested by cone maggots may be due to preexisting entry points or to the increased nutritive value of infested cones (Fidgen and Sweeney 1996). Detection of maggot-infested cones by *D. abietivorella* may be mediated by an alteration of the cones' monoterpene profile, which acts as a kairomone to attract females for oviposition or larvae for feeding (Fidgen and Sweeney 1996). Early-instar *D. amatella* larvae infest loblolly pine cones previously infested, though not killed, by *D. disclusa* and the cone midge *Resseliella silvana* (Felt) (Diptera: Cecidomyiidae) (Hanula *et al.* 1985).

Dioryctria species magnify the impact of disease damage through a preference for feeding on diseased tissues. Southern cone rust, *Cronartium strobilinum* (Arthur) Hedge and Hahn (Cronartiaceae), affects first-year cones of slash and longleaf pines (Merkel 1958). *Dioryctria amatella* and *D. ebeli* larvae occur in higher abundance on rust-infected than on disease-free first-year cones. As *Dioryctria* populations increase on these cones and infected first-year cones die, larvae migrate to second-year cones to continue feeding. Higher larval infestations occur on second-year cones on the same branches as rust-infected first-year cones than on branches with disease-free first-year cones. Seed losses due to rust are amplified by *Dioryctria* infestation on second-year cones (Merkel 1958).

Cone-boring by *Dioryctria* species also increases cone vulnerability to pathogens. Diplodia tip blight, *Sphaeropsis sapinea* (Fr.) Dyko and B. Sutton (*incertae sedis*), is a common fungal pathogen that affects shoots, twigs, and cones of conifer trees (Nicholls and Ostry 1990). The occurrence of *S. sapinea* in closed red pine cones increased from 9% to 56% when *D. resinosella* (*zimmermani* group) was also present. Holes bored in closed cones can provide a point of entry for the conidia, and cone damage may release the fungus from dormancy (Feci *et al.* 2003).

The presence of pathogens such as blister rusts may provide polyphagous facultative cone-feeders with another nutrient source to maintain populations between mast years. *Dioryctria amatella*, *D. abietivorella*, and *D. cambiicola* attack pines infected with rust diseases caused by *Cronartium* Fries (Cronartiaceae) species (Coulson and Franklin 1970*a*, 1970*b*; Furniss and Carolin 1977; Rocchini *et al.* 1999). The presence of *D. cambiicola* was positively associated with the presence of the *C. coleosporioides* Arthur in lodgepole pine provenance trials in western Canada. Larvae feed at the perimeter of the rust blisters in association with fungal hyphae; the benefits of fungal feeding for *D. cambiicola* fitness are unknown (Rocchini *et al.* 1999). Measurements of larval and adult survival as well as fecundity are required to ascertain the potential benefits of hyphal feeding.

Monitoring

Management of *Dioryctria* species in conifer seed orchards depends on knowledge of the presence of adult or larval stages in the seed-production area (Fig. 4). The phenology of several pest complexes has been investigated. Schowalter (1994) exposed Douglas-fir cones as oviposition substrates to potential pests for discrete periods throughout the summer in western Oregon. Infestations by *D. abietivorella* larvae are highest when cones are exposed between mid-April and mid-May; infestations from cone exposure through mid-August are lower (Schowalter 1994). May and June are the primary months of cone infestation by *D. auranticella* larvae (Pasek and Dix 1989).

Monitoring of *Dioryctria* larvae is conducted either by scouting for frass on cones (*e.g.*, Rosenberg and Weslien 2005) or through cone dissections to recover larvae (*e.g.*, Dormont and Roques 1999). No quantitative plans exist for sampling larvae, although indirect estimates of infestation rates can be derived from repeated examinations of cones throughout their development. This method is used to estimate cone damage and survival in seed orchards in the southern United States (DeBarr *et al.* 1975). Throughout development, tagged first- and second-year cones are repeatedly checked for damage and mortality, thereby taking into account damage due to *Dioryctria* (DeBarr *et al.* 1975). Sequential sampling to quantify stand infestation levels is not economical but can be used to determine whether cone collection is worthwhile (Kozak 1964). Larval identification during sampling is critical, and a dichotomous key to the final instars of six cone-infesting *Dioryctria* species in eastern North America is available (Leidy and Neunzig 1989). Morphological keys do not exist for other species or earlier instars, though it should now be possible to identify species groups and most species by means of molecular techniques (Roe *et al.* 2006) (Fig. 4).

Ultraviolet light is attractive to a broad range of *Dioryctria* species (Fig. 4), and adults are monitored successfully with light traps. In British Columbia, black-light traps are used to monitor flight activity of male and female *D. abietivorella* as well as members of the *auranticella*, *ponderosae*, and *zimmermani* groups (unpublished data). McLeod and Yearian (1982) deployed black-light traps to monitor five *Dioryctria* species in Arkansas. Trap catch of *D. amatella* coincides with adult eclosion from pupae in mature cones. Black-light traps are also used in Georgia to determine the flight phenology of four *Dioryctria* species (Yates and Ebel 1975). Roe *et al.* (2006) used ultraviolet-light traps to collect adults of the *schuetzeella* group in California. In all species except *D. pygmaeella*, male catch exceeds female catch in light traps (McLeod and Yearian 1982).

Sex pheromones of several *Dioryctria* species have been developed as monitoring tools. Several commercially available traps baited with a pheromone attractive to male *D. abietivorella* (Strong *et al.* 2008) were tested at different positions in the canopy. Diamond traps (ConTech Enterprises Inc., Delta, British Columbia) positioned near the tops of trees capture the largest number of male moths (Strong *et al.* 2008). Significantly more males are captured when traps are positioned near the tops of trees: 4 m above ground in topped seed-orchard trees, 8 m in untopped seed-orchard trees, and 22 m in wild-stand trees (unpublished data). The similarity of pheromone components and blends used by four southern Nearctic *Dioryctria* species led to both interspecific cross-attraction and inhibition of adult male attraction to traps baited with synthetic pheromone (Hanula *et al.* 1984*a*). Attraction of male moths from three different species groups (*D. disclusa*, *D. merkeli*, and *D. clarioralis*) to one lure allows these species to be monitored with a single lure in a single trap. In the same orchards, *D. amatella* (*zimmermani* group) must be monitored with different lures in separate traps because of an inhibitory effect on the pheromone response of other *Dioryctria* species mediated by one component of the *D. amatella* pheromone. Hanula *et al.* (1984*c*) found that pheromone-baited Pherocon 1C traps caught more *D. amatella* than traps of three other designs tested. Although adult males are captured in pheromone-baited traps, trap capture has not yet been incorporated into integrated pest management programs targeting these species (Fig. 4). Effective monitoring using sex pheromones will depend on the composition of the species assemblages present. It remains to be determined whether capture in pheromone-baited traps is related to levels of larval damage and could therefore be developed as a decision-making tool for orchard-pest managers.

Decision-making

In integrated pest management protocols, action thresholds based upon monitoring results are typically used to make decisions (Pedigo 1996) (Fig. 4). Without the development of quantitative methods to monitor eggs, larvae, or adults, action thresholds cannot be devised for pestiferous *Dioryctria* species. Currently, timing of pesticide applications could be based on information about adult flight phenology, but no such protocols have been developed. A day-degree model has been developed for *D. amatella*, based on accumulations above a threshold temperature of 11 °C initiated with a biofix of five male moths in pheromone traps (Hanula *et al.* 2002). No other decision-making model for managing seed-feeding *Dioryctria* species has been published to date.

Control

Semiochemicals: sex pheromones

Pheromone-based mating disruption is one method that may prove useful for controlling infestations of seed-feeding *Dioryctria* species (Fig. 4). Similarity in pheromone composition among species (Table 3) may facilitate multi-species mating disruption of sympatric *Dioryctria* species. DeBarr *et al.* (2000) explored the possibility of using pheromone-based mating disruption to control three *Dioryctria* species in loblolly pine seed orchards in Georgia. Three polyvinyl chloride rods releasing a mean concentration of 0.458 mg ha^{-1} day^{-1} of synthetic pheromone per tree in 1.2 ha plots resulted in reductions of 91%, 96.7%, and 99.5% in trap catches of two *zimmermani*-group species (*D. amatella* and *D. merkeli*) and one *auranticella*-group species (*D. disclusa*), respectively, compared with untreated plots. Disruption of *D. merkeli* and *D. disclusa* pheromone communication was achieved using *Z*9–14:Ac; disruption of *D. amatella* pheromone communication was achieved using *Z*9–11:Ac. Larval densities and seed losses were not compared between treatments (DeBarr *et al.* 2000). Large-scale implementation of mating disruption to control *Dioryctria* has not been reported.

Semiochemicals: host-plant volatiles

Information about semiochemical cues used by Palearctic *Dioryctria* species for locating hosts and oviposition sites could be exploited for the management of pestiferous North American populations (Fig. 4). Host-produced semiochemicals have been used to control infestations by *D. mutatella* Fuchs and Fazekas in the French Alps (Dormont *et al.* 1997). The cones of mountain pine, *Pinus uncinata* Mill. *ex* Mirb., are more heavily attacked by *D. mutatella* than those of Swiss stone pine and also have different volatile terpene profiles (Dormont *et al.* 1997). Extracts of Swiss stone pine sprayed on cones of mountain pine reduce cone damage by *D. mutatella* from 14.1% to zero, and infestation by all seed-feeding pests from 31% to zero. Large-scale control that utilizes push–pull management strategies will also rely on information derived from research on host-preference hierarchies.

Genetic host resistance

Genetic host resistance to *Dioryctria* attack can be exploited in control regimes (Fig. 4).

Loblolly pine seed orchards show clonal variation in cone-attack rates by southern Nearctic *Dioryctria* species (*D. amatella*, *D. clarioralis*, *D. disclusa*, and *D. merkeli*) that range from zero to 67% (Askew *et al.* 1985). Genetic variation in host resistance allows for the possibility of breeding for resistance, in particular because cone-infestation rates are not correlated with performance values for tree height or diameter. Even without extensive breeding efforts, sprays could be directed to only the most susceptible genotypes in order to reduce total spray load in an orchard. Fodor (1978) determined the heritability of resistance to *D. abietella* in a Polish pine orchard to be between 0.66 and 0.86, values that would support the development of a breeding program for *Dioryctria* resistance. However, there is a negative correlation between resistance level and cone production, and no report on breeding effort targeting host resistance to *Dioryctria* has been published.

Parasitoids

Hymenopteran species in the families Braconidae, Eulophidae, Ichneumonidae, Ptermalidae, and Trichogrammatidae, as well as tachinid flies, parasitize cone- and seed-feeding *Dioryctria* species (Table 5). Ichneumonids and eulophids parasitize *D. abietivorella* larvae (Lyons 1957; Bradley 1974). Larvae of seven species of *Elachertus* Spinola (Hymenoptera: Eulophidae) emerged from one mature *D. abietivorella* larva (Lyons 1957). Though there are few reports, parasitism rates may be as high as 18.8% in *D. amatella* in loblolly pine seed orchards (Mihelcic *et al.* 2003) and 27.0% in northern Florida slash pine (Belmont and Habeck 1983). *Phanerotoma* Wesmael (Hymenoptera: Braconidae) was the most common parasitoid genus associated with *D. ebeli* in slash pine orchards in northern Florida (Belmont and Habeck 1983). Of *D. disclusa* pupae sampled in Ontario red pine orchards, 48% were parasitized (Lyons 1957). Very little biological information about the parasitoids of *Dioryctria* is available, although Belmont and Habeck (1983) did record detailed life-history information for *Hyssopus rhyacioniae* Gahan (Hymenoptera: Eulophidae) and a new species of *Pediobius* Walker (Hymenoptera: Eulophidae) reared from *D. amatella*.

The impact of natural enemies in the control of *Dioryctria* populations requires further documentation, including species identification, geographic and host ranges, life history, phenology, and host mortality rates. Parasitoid complexes should be identified and shifts in community composition throughout the season resolved. Hyperparasitoids, such as *Itoplectis conquisitor* (Say) (Hymenoptera: Ichneumonidae) (Goulet and Huber 1993), *Elasmus meteori* Ashmead (Hymenoptera: Elasmidae) (Merkel 1982), and a species of *Pediobius* Walker (Belmont and Habeck 1983), could disrupt biological-control efforts, and should be identified. At this time natural enemies have not been incorporated into biological control programs against *Dioryctria* species (Fig. 4).

Pathogens

Pathogenic microorganisms infect several *Dioryctria* species (Table 5). In their study of pathogenic microorganisms in *D. amatella*, Mihelcic *et al.* (2003) found that the fungus *Beauveria bassiana* (Balsamo) Vuillemin (Clavicipitaceae), a granulosis virus, and a microsporidian species infected 0.4%, 2.4%, and 5.2% of sampled larvae, respectively. In laboratory trials, *B. bassiana* and the virus were virulent against all larval stages, and the microsporidia caused high levels of mortality in early-instar larvae. Although rates of natural infection with *B. bassiana* were low, a sprayable product is commercially available (Laverlam International Corporation, Butte, Montana) and has potential for development as a biopesticide in this system. Two additional pathogens, *Hirsutella satumaensis* Aoki and *Metarhizium anisopliae* (Mechnikov) Sorokin (Clavicipitaceae), have been recovered from field-collected Palearctic *Dioryctria* species (Mihelcic *et al.* 2003). More work is needed to fully identify pathogens of North American *Dioryctria* species that could be candidates for use in biological control (Fig. 4).

Biopesticides

The commercially available biopesticide *Bacillus thuringiensis* Berliner subsp. *kurstaki* (Bacillaceae) (Btk) has been tested against various *Dioryctria* species (Fig. 4). *Dioryctria abietivorella* larvae in all stadia are highly and

Table 5. Reported natural enemies of North American cone-feeding *Dioryctria* species.

Dioryctria species	Natural enemy	Reference(s)
***abietella* group**		
abietivorella	*Elachertus* Spinola species [a], *Pediobius* Walker species [a], *Exeristes comstockii* Cresson[b], *Exochus evetriae* Rohwer[b], *Scambus longicorpus occidentalis* Walley[b], unidentified tachinid[c]	Lyons 1957; Bradley 1974
ebeli	*Hyssopus rhyacioniae* Gahan [a], *Agathis* Latreille species[d], *Apanteles* Förster species[d], *Apanteles bushnelli* Muesebeck[d], *Macrocentrus* Curtis species[d], *Phanerotoma* Wesmael species[d], *Trichogramma* Westwood species[e] *Leskiomina tenera* Wiedemann[c], *Phrynofrontina* Townsend species[c], *Xanthophyto* Townsend species[c]	Ebel 1965; Belmont and Habeck 1983
***auranticella* group**		
auranticella	*Elachertus argissa* Walker [a], *Exeristes comstockii*[b], *Exochus turgidus* Holmgren[b], *Horogenes* Förster species[b], *Ichneumon brunneri* Rohwer[b], *Scambus* species poss. *annulatus* (Kiss) [b], *Temelucha platynotae* Cushman [b], *Meteorus* Haliday species[d], *Meteorus indagator* Riley[d], *Habrobracon cushmani* Muesebeck[d], *Dibrachys cavus* Walker[f], *Nemorilla pyste* Walker[c]	Raizenne 1952; Bradley 1974; Pasek and Dix 1989
disclusa	*Calliephialtes comstockii* Cresson[b], *Coelichneumon* Thomson species[b], *Exeristes comstockii* Cresson[b], *Exochus turgidus*[b], *Horogenes* species[b], *Ichneumon brunneri*[b], *Microtypus* Ratzeburg species[d] , *Apanteles* species[d], *Apanteles bushnelli*[d], *Bracon rhyacioniae* Muesebeck[d], *Meteorus indagator*[d], *Meteorus tetralophae* Muesebeck[d], *Dibrachys cavus*[f], *Eupelmus cyaniceps* var. *amicus* Girault[g], unidentified tachinid[c]	Raizenne 1952; Lyons 1957; Farrier and Tauber 1953; Neunzig *et al.* 1964; Bradley 1974
***baumhoferi* group**		
clarioralis	*Hyssopus rhyacioniae* [a], *Campoplex* Gravenhorst species[b], *Apanteles bushnelli*[d], *Macrocentrus* species[d], *Phrynofrontina* species[c], *Beauvaria bassiana* (Balsamo) Vuillemin[h]	Ebel 1965; Belmont and Habeck 1983
***pygmaeella* group**		
pygmaeella	*Elasmus meteori* Ashmead [a], *Calliephialtes grapholithae* (Cresson) [b], *Apanteles* species[d], *Bracon* F. species[d], *Macrocentrus delicates* Cresson[d], *Macrocentrus dioryctriae* Muesebeck[d] , *Brachymeria molestae* Burks[i], *Genea* Rondani species[c], *Lixophaga* Townsend species[c]	Merkel 1982
***schuetzeella* group**		
reniculelloides	*Pimplopterus* Ashmead species[b], *Pimplopterus parvus* Cresson[b], *Campoplex validus* Cresson[b], *Campoplex* species[b], *Horogenes kiehtani* Viereck[b], *Scambus hispae* Harris[b], *Itoplectis conquisitor* Say[b], *Glypta fumiferanae* Viereck[b], *Phytodietus vulgaris* Cresson[b], *Apanteles* species[d], *Apanteles canarsiae* Ashmead[d], *Apanteles fumiferanae* Viereck[d], *Bracon politventris* Cushman[d], *Bracon gelechiae* Ashm.[d], *Meteorus trachynotus* Viereck[d], *Phryxe pecosensis* Townsend[c], *Eumea caesar* Aldrich[c]	Raizenne 1952; McLeod and Daviault 1963

Table 5 (*concluded*).

Dioryctria species	Natural enemy	Reference(s)
***zimmermani* group**		
amatella	*Hyssopus rhyacioniae* [a], *Pediobius* species [a], *Campoplex* species[b], *Campoplex conocola* Rohwer[b], *Exeristes comstockii*[b], *Exochus turgidus*[b], unidentified Lissonotini[b], *Lissonota amatella* Townes[b], *Agathis* species[d], *Bracon* species[d], *Macrocentrus* species[d], *Macrocentrus dioryctriae*[d], *Phrynofrontina* species[c], *Xanthophyto* species[c], *Beauvaria bassiana*[h], granulosis virus[j], unidentified microsporidia	Ebel 1965; Neunzig *et al.* 1964; Belmont and Habeck 1983; Mihelcic *et al.* 2003
cambiicola	*Hyssopus rhyacioniae* [a], *Campoplex conocola*[b], unidentified tachinid[c]	Lyons 1957
taedivorella	*Hyssopus rhyacioniae* [a]	Neunzig *et al.* 1964

[a] Hymenoptera: Eulophidae.
[b] Hymenoptera: Ichneumonidae.
[c] Diptera: Tachinidae.
[d] Hymenoptera: Braconidae.
[e] Hymenoptera: Trichogrammatidae.
[f] Hymenoptera: Pteromalidae.
[g] Hymenoptera: Eupelmidae.
[h] Clavicipitaceae.
[i] Hymenoptera: Chalcididae.
[j] Baculoviridae.

equally susceptible to Btk (Trudel *et al.* 1997). First-instar larvae of *D. amatella* are highly susceptible to Btk in laboratory bioassays; older instars are less susceptible but once infected, die more quickly than younger larvae (McLeod *et al.* 1982). McLeod *et al.* (1984) field-tested Btk sprays on second-year cones of loblolly pine in Oklahoma. Btk application 1 week after *D. amatella* are first caught in pheromone traps increases cone survival by approximately 18% and seed set per cone by 48%. No significant protection from *D. amatella* occurs if Btk is applied 2 weeks after first trap catch, suggesting that timing is critical to the success of Btk application (McLeod *et al.* 1984).

The efficacy of Btk has been most thoroughly tested against *D. abietella* (*abietella* group) in Norway spruce seed orchards in Sweden. Three applications, starting within 1 week of the onset of adult flight, reduce the incidence of cone infestation by 65% (Weslien 1999). Highly susceptible first-instar larvae probably ingest Btk as they penetrate cones, and older larvae may be exposed as they move between cones (Weslien 1999). To test the hypothesis that Btk is more persistent within young cones than on exposed cone surfaces, Glynn and Weslien (2004) tested sprays when the female strobili were open. In this trial, *Dioryctria* infestation was reduced by approximately 50% in sprayed plots. Cone damage can be reduced by between 30% and 60% using commercial application equipment in 0.3 ha plots (Rosenberg and Weslien 2005).

Insecticides

Currently, the use of synthetic pesticides is the main control strategy for managing *Dioryctria* populations in conifer seed orchards (Fig. 4). In laboratory assays comparing contact toxicity of 17 insecticides against *D. amatella*, 8 were more toxic than azinphosmethyl, the only insecticide registered against this species at that time (DeBarr and Fedde 1980). Two organophosphosphate and three pyrethroid insecticides are ovicidal to *D. amatella* at any point during egg development, while two other organophosphates are ovicidal only to 5-day-old eggs (McLeod and Yearian 1983). Timed applications of effective ovicides would be a useful management tool because cone-dwelling larvae escape later contact insecticide applications.

An advantage of systemic insecticides, which can translocate into cones and kill seed-feeding insects, is a reduction in nontarget mortality. Six systemic insecticides tested against *D. amatella* have low contact toxicity in laboratory assays but are effective in the field, which suggests that the mode of action is through ingestion

(DeBarr and Fedde 1980). The efficacy of injecting loblolly pine stems with emamectin benzoate (EB), imidacloprid, or a combination of EB and thiamethoxam was tested in Texas (Grosman *et al.* 2002). A single EB application reduced damage from *Dioryctria* species by 94%–97% over a 2-year period; imidacloprid significantly reduced damage only during the season of application. In a comparison of injections and dripline drenches of several systemic insecticides to control *D. abietella* attacking Himalayan spruce, *Picea smithiana* (Wall.) Boiss., in northern India, 13.5% of cones were infested after stem injections with monocrotophos, whereas 87.5% in control plots were infested (Bhandari *et al.* 2006*a*).

Broadcast sprays of contact insecticides are the most commonly used application technique against a variety of *Dioryctria* species. After treatment of western white pine seed orchards in Idaho to target *D. abietivorella* with one or two high-volume ground applications of fenvalerate, 13.6% of cones were infested (and seed yield was doubled) compared with 46.6% in untreated control plots (Haverty *et al.* 1986). Five ground applications of azinphos-methyl, fenvalerate, and permethrin applied by airblast sprayer at monthly intervals reduced seed losses due to *Dioryctria* species in loblolly pine seed orchards by 52%–67% (Nord *et al.* 1985). Aerial applications of fenvalerate increased cone survival from 14% in unsprayed orchards to as high as 86% in treated orchards (Nord *et al.* 1985). Two ground applications of fenvalerate with an airblast sprayer can significantly reduce cone damage due to *D. amatella*, though a single application does not successfully control the pest (Hanula *et al.* 2002). The use of a day-degree model to time applications allows the number of targeted applications of fenvalerate against *D. amatella* to be reduced (Hanula *et al.* 2002). Future research on chemical insecticides should identify the effects on nontarget species present in seed orchards, including sublethal effects and secondary pest upsurges.

Future directions

Research on factors influencing population distributions on spatial and temporal scales is needed to build sound management strategies. Resolution of factors that influence landscape-level distributions of individuals in habitats as mediated by host-finding behaviour, pre- and post-mating dispersal, and overwintering behaviour should be a high priority because of their importance in monitoring and management. On a finer scale, at the tree level, what influences egg or larval distribution is not fully understood. Fine-scale distribution may be moderated by cues that stimulate or deter oviposition and feeding. Intra- and inter-specific interactions such as predation and competition could also affect fine-scale distribution.

Research to address phenological and genetic diversity in *Dioryctria*, including identification of geographic pheromone races, host races, and pesticide resistance, is also necessary to ensure the efficacy of species-specific control methods. Several avenues of phylogenetic research within *Dioryctria*, particularly in the *abietella* group, are needed. First, a thorough population genetic survey of *D. abietivorella* throughout its range is needed to quantify intraspecific variation, given the geographic variability of pheromone response (Grant *et al.* 2009) and larval host associations. Second, species limits between *D. abietivorella* and *D. ebeli* need to be examined using a variety of molecular (*e.g.*, microsatellites), morphological (*e.g.*, wing-pattern variation), and behavioural traits (*e.g.*, larval host-plant association) using an integrative approach as described for *D. reniculelloides* and *D. pseudotsugella* (Roe and Sperling 2007). Third, a well-supported phylogeny of *Dioryctria* species groups would be helpful for forming hypotheses about the diversification of the genus; this will require more comprehensive representation of the known species and their genomic differences.

Successful management of cone-feeding *Dioryctria* species relies on sound monitoring protocols, decision-making methods, and appropriate control strategies (Fig. 4). Integrated pest management requires the creation of damage-prediction and monitoring methods, as well as an understanding of population dynamics and density—damage relationships. These measures allow the development of economic-injury thresholds and quantitative decision-making. Integration of predictive methods, such as economic-injury thresholds, into control strategies can permit biologically based timing rather than calendar-based spray applications.

Pheromone-based control tactics such as mating disruption or attract-and-kill require information derived from reproductive-behaviour studies. Additional research on *Dioryctria* reproductive strategies focusing on factors that influence female fecundity (*e.g.*, larval feeding, male-derived nutrients), mating frequency, and oviposition is required in order to design and improve management strategies. The influence of nutrition, including nectar sources for adults, on development rates and reproductive potential is unknown. Semiochemical-based control that exploits important host-finding cues could be used to monitor females and manipulate host-finding and reproductive behaviours. Further development of integrated pest management programs requires research to incorporate pathogens such as Btk into *Dioryctria* management. The effect of natural enemies (insect, avian, and mammalian) should be promoted by developing their habitats.

In conclusion, effective control of pestiferous *Dioryctria* species should include multiple methods that serve to manipulate and (or) exploit pest behaviour and reduce the current reliance on highly toxic broad-spectrum pesticides to control *D. abietivorella*. This can be achieved through (*i*) correct identification of target insects through increased understanding of diagnostic molecular and morphological traits, (*ii*) full documentation of the life-history requirements and interactions of *Dioryctria* species within and between trophic levels, and (*iii*) a better understanding of the integration of the heterogeneous evolutionary, ecological, and environmental factors that promote the adaptive flexibility of *Dioryctria* coneworms that underlies their economic impact.

Acknowledgements

Funding was provided by the Forest Genetics Council of British Columbia (research grant No. RE1051Y037), the Kalamalka Forestry Centre of the British Columbia Ministry of Forests and Range, and the University of Alberta. F.A.H.S. and M.L.E. acknowledge funding from their respective Discovery Grants from the Natural Sciences and Engineering Research Council of Canada. D. Miller, A. Mangini, and an anonymous reviewer provided helpful suggestions on an earlier version of the manuscript.

References

Amsel, H.G. 1962. Neue Microlepidoptera aus Guatemala. Zeitschrift für angewandte Entomologie, **49**: 392–398.

Asher, W.C. 1970. Olfactory response of *Dioryctria abietella* (Lepidoptera: Phycitinae) to slash pine cones. Annals of the Entomological Society of America, **63**: 474–476.

Askew, G.R., Hedden, R.L., and DeBarr, G.L. 1985. Clonal variation in susceptibility to coneworms (*Dioryctria* spp.) in young loblolly-pine seed orchards. Forest Science, **31**: 794–798.

Belmont, R.A., and Habeck, D.H. 1983. Parasitoids of *Dioryctria* spp. (Pyralidae: Lepidoptera) coneworms in slash pine seed production areas of north Florida. Florida Entomologist, **66**: 399–407. doi:10.2307/3494013.

Bhandari, R.S., Dobhal, B., and Pande, S. 2006*a*. Effect of cone worm, *Dioryctria abietella* Denis and Schiffermuller (Lepidoptera: Pyralidae) on the seed efficiency of *Pinus wallichiana*. Indian Forester, **132**: 1493–1498.

Bhandari, R.S., Pande, S., Joshi, M.C., Zaidi, S.M.H., Rawat, J.M.S., and Kumar, V. 2006*b*. Control of cone worm, *Dioryctria abietella* Denis and Schifferműeller (Lepidoptera: Pyralidae) in seed production areas of spruce, *Picea smithiana* Boiss by systemic insecticides. Indian Forester, **132**: 1041–1046.

Blanchard, A., and Knudson, E.C. 1983. A new species of *Dioryctria* Zeller (Lepidoperta: Pyralidae) from Texas. Proceedings of the Entomological Society of Washington, **85**: 116–120.

Bradley, G.A. 1974. Parasites of forest Lepidoptera in Canada. Part 1. Subfamilies Metopiinae and Pimplinae (Hymenoptera: Ichneumonidae). Canadian Forestry Service, Environment Canada, Ottawa, Ontario.

Coates, D.K. 1994. Ecology and silviculture of Interior spruce in British Columbia. FRDA report 220. Canada-British Columbia Partnership Agreement of Forest Resource Development: FRDA II: Canadian Forest Service, Pacific Forestry Centre and B.C. Ministry of Forests.

Coulson, R.N., and Franklin, R.T. 1970*a*. The biology of *Dioryctria amatella* (Lepidoptera: Phycitidae). The Canadian Entomologist, **102**: 679–684. doi:10.4039/Ent102679-6.

Coulson, R.N., and Franklin, R.T. 1970*b*. Occurrence of *Dioryctria amatella* and other insects in *Cronartium fusiform* cankers. The Canadian Entomologist, **102**: 353–357. doi:10.4039/Ent102353-3.

DeBarr, G.L., and Berisford, C.W. 1981. Attraction of webbing coneworm males to female sex pheromone. Environmental Entomology, **10**: 119–121.

DeBarr, G.L., and Fedde, V.H. 1980. Contact toxicity of 17 insecticides to larvae of *Dioryctria amatella* (Lepidoptera: Pyralidae). The Canadian Entomologist, **112**: 521–523. doi:10.4039/Ent112521-5.

DeBarr, G.L., Barber, L.R., and Wilkinson, R.C. 1975. Within-crown distribution of cone and seed insect damage to slash pine flowers, conelets, and cones. Florida Entomologist, **58**: 281–288. doi:10.2307/3493692.

DeBarr, G.L., Hanula, J.L., Niwa, C.G., and Nord, J.C. 2000. Synthetic pheromones disrupt male *Dioryctria* spp. moths in a loblolly pine seed orchard. The Canadian Entomologist, **132**: 345–351. doi:10.4039/Ent132345-3.

Dormont, L., and Roques, A. 1999. A survey of insects attacking seed cones of *Pinus cembra* in the Alps, the Pyrenees and Massif Central. Journal of Applied Entomology, **123**: 65–72. doi:10.1046/j.1439-0418.1999.00318.x.

Dormont, L., Roques, A., and Malosse, C. 1997. Efficiency of spraying mountain pine cones with oleoresin of Swiss stone pine cones to prevent insect attack. Journal of Chemical Ecology, **23**: 2261–2274. doi:10.1023/B:JOEC.0000006672.05861.6c.

Du, Y.L., Roe, A.D., and Sperling, F.A.H. 2005. Phylogenetic framework for *Dioryctria* (Lepidoptera: Pyralidae: Phycitinae) based on combined analysis of mitochondrial DNA and morphology. The Canadian Entomologist, **137**: 685–711. doi:10.4039/N05-033.

Ebel, B.H. 1965. The *Dioryctria* coneworms of north Florida pines (Lepidoptera: Phycitinae). Annals of the Entomological Society of America, **58**: 623–630.

Evenden, M.L., G.J.R. Judd, and Borden, J.H. 1999. A synomone imparting distinct sex pheromone communication channels for *Choristoneura rosaceana* (Harris) and *Pandemis limitata* (Robinson) (Lepidoptera: Tortricidae). Chemoecology, **9**: 73–80. doi:10.1007/s000490050036.

Farrier, M.H., and Tauber, O.F. 1953. *Dioryctria disclusa* Heinrich, n. sp. (Phycitidae) and its parasites in Iowa. Iowa State University Journal of Science, **27**: 495–507.

Fatzinger, C.W. 1981. Activity rhythms, influence of host plant on mating and oviposition, and rearing of the southern pine coneworm (Lepidoptera: Pyralidae). Florida Entomologist, **64**: 506–515. doi:10.2307/3494407.

Fatzinger, C.W., and Asher, W.C. 1971*a*. Observations on the pupation and emergence behavior of *Dioryctria abietella* (Lepidoptera: Pyralidae (Phycitinae)). Annals of the Entomological Society of America, **64**: 413–418.

Fatzinger, C.W., and Asher, W.C. 1971*b*. Mating behavior and evidence of a sex pheromone of *Dioryctria abietella* (Lepidoptera: Pyralidae (Phycitinae)). Annals of the Entomological Society of America, **64**: 612–620.

Feci, E., Smith, D., and Stanosz, G.R. 2003. Association of *Sphaeropsis sapinea* with insect-damaged red pine shoots and cones. Forest Pathology, **33**: 7–13.

Fidgen, L.L., and Sweeney, J.D. 1996. Fir coneworm, *Dioryctria abietivorella* (Grote) (Lepidoptera: Pyralidae), prefer cones previously exploited by the spruce cone maggots *Strobilomyia neanthracina* Michelsen and *Strobilomyia appalachensis* Michelsen (Diptera: Anthomyiidae). The Canadian Entomologist, **128**: 1221–1224. doi:10.4039/Ent1281221-6.

Fodor, S. 1978. Possibilities of selecting for resistance to pine cone pests. Agrartudomanyi Kozlemenyek, **37**: 275–277.

Furniss, R.L., and Carolin, V.M. 1977. Western forest insects. United States Department of Agriculture, Forest Service, Washington, D.C.

Glynn, C., and Weslien, J. 2004. *Bacillus thuringiensis* variety *kurstaki* × *aizawai* applied to spruce flowers reduced *Dioryctria abietella* (Lepidoptera: Pyralidae) infestation without affecting seed quality. Journal of Economic Entomology, **97**: 1836–1841. PMID:15666734 doi:10.1603/0022-0493-97.6.1836.

Goulet, H., and Huber, J.T. 1993. Hymenoptera of the world: an identification guide to families. Agriculture Canada, Ottawa, Ontario.

Grant, G.G., Prevost, Y.H., Slessor, K.N., King, G.G.S., and West, R.J. 1987. Identification of the sex pheromone of the spruce coneworm, *Dioryctria reniculelloides* (Lepidoptera: Pyralidae). Environmental Entomology, **16**: 905–909.

Grant, G.G., Katovich, S.A., Hall, D.J., Lombardo, D.A., and Lessor, K.N. 1993. Sex pheromone identification and trapping of *Dioryctria resinosella* (Lepidoptera: Pyralidae). Environmental Entomology, **22**: 154–161.

Grant, G.G., Millar, J.G., and Trudel, R. 2009. Pheromone identification of *Dioryctria abietivorella* (Lepidoptera: Pyralidae) from an eastern North American population: geographic variation in pheromone response. The Canadian Entomologist, **141**: 129–135. doi:10.4039/n09-008.

Grinnell, J. 1924. Geography and evolution. Ecology, **5**: 225–229. doi:10.2307/1929447.

Grosman, D.M., Upton, W.W., McCook, F.A., and Billings, R.F. 2002. Systemic insecticide injections for control of cone and seed insects in loblolly pine seed orchards — 2 year results. Southern Journal of Applied Forestry, **26**: 146–152.

Grote, A.R. 1878. Preliminary studies on North American Pyralidae I. Bulletin of the United States Geological and Geographical Survey of the Territories, Washington, **4**: 669–705.

Grote, A.R. 1880. A new *Pinipestis*. North American Entomologist, Buffalo, **1**: 67.

Hanula, J.L., Berisford, C.W., and DeBarr, G.L. 1984*a*. Pheromone cross-attraction and inhibition among four coneworms, *Dioryctria* spp. (Lepidoptera: Pyralidae) in a loblolly pine seed orchard. Environmental Entomology, **13**: 1298–1301.

Hanula, J.L., DeBarr, G.L., and Berisford, C.W. 1984*b*. Oviposition behavior and temperature effects on egg development of the southern pine coneworm, *Dioryctria amatella* (Lepidoptera: Pyralidae). Environmental Entomology, **13**: 1624–1626.

Hanula, J.L., DeBarr, G.L., Harris, W.M., and Berisford, C.W. 1984*c*. Factors affecting catches of male coneworms, *Dioryctria s*pp. (Lepidoptera, Pyralidae), in pheromone traps in southern pine seed orchards. Journal of Economic Entomology, **77**: 1449–1453.

Hanula, J.L., DeBarr, G.L., and Berisford, C.W. 1985. Adult activity of *Dioryctria amatella* (Lepidoptera: Pyralidae) in relation to development of immature stages in loblolly pine cones. Environmental Entomology, 14: 842–845.

Hanula, J.L., DeBarr, G.L., Weatherby, J.C., Barber, L.R., and Berisford, C.W. 2002. Degree-day model for timing insecticide applications to control *Dioryctria amatella* (Lepidoptera: Pyralidae) in loblolly pine seed orchards. The Canadian Entomologist, **134**: 255–268. doi:10.4039/Ent134255-2.

Haverty, M.I., Shea, P.J., and Stipe, L.E. 1986. Single and multiple applications of fenvalerate to protect western white pine cones from *Dioryctria abietivorella* (Lepidoptera: Pyralidae). Journal of Economic Entomology, **79**: 158–161.

Hedlin, A.F. 1974. Cone and seed insects of British Columbia. Report BC-X-90, Canadian Forestry Service, Environment Canada, Victoria, British Columbia.

Hedlin, A.F., Yates, H.O., III, 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, Environment Canada, Ottawa, Ontario, United States Forest Service, Washington, D.C., and Secretaría de Agricultura y Recursos Hidráulicos, Mexico.

Heinrich, C. 1956. American moths of the subfamily Phycitinae. United States National Museum Bulletin No. 207.

Janzen, D.H. 1971. Seed predation by animals. Annual Review of Ecology and Systematics, **2**: 465–492. doi:10.1146/annurev.es.02.110171.002341.

Keen, F.P. 1952. Insect enemies of western forests. United States Department of Agriculture Miscellaneous Publication No. 273. Pp. 20–23.

Kegley, S., Sturdevant, N., Stein, J., Willhite, B., Flanagan, P., Weatherby, J., and Marsden, M. 2001. Cone and seed insects and their impact on whitebark pine. Forest Health Protection Report 01–6, United States Department of Agriculture, Forest Service, Northern Region, Missoula, Montana.

Kelly, D. 1994. The evolutionary ecology of mast seeding. Trends in Ecology and Evolution, **9**: 465–470. doi:10.1016/0169-5347(94)90310-7.

Knölke, S., Eralcher, S., Hausmann, A., Miller, M.A., and Segerer, A. 2005. A procedure for combined genitalia dissection and DNA extraction in Lepidoptera. Insect Systematics and Evolution, **35**: 401–409.

Kozak, A. 1964. Sequential sampling for improving cone collection and studying damage by cone and seed insects in Douglas fir. Forestry Chronicle, **40**: 210–218.

Lee, K.Y., and Lee, C.Y. 1994. A study on the cone insects of some *Pinus*. Research Bulletin of the Experiment Forests, Kangweon National University, **14**: 139–151.

Leidy, N.A., and Neunzig, H.H. 1989. Taxonomic study of the larvae of six eastern North American *Dioryctria* (Lepidoptera: Pyralidae: Phycitinae). Proceedings of the Entomological Society of Washington, **91**: 325–341.

Löfstedt, C., Vanderpers, J.N.C., Lofqvist, J., and Lanne, B.S. 1983. Sex pheromone of the cone pyralid *Dioryctria abietella*. Entomologia Experimentalis et Applicata, **34**: 20–26. doi:10.1007/BF00300895.

Lyons, L.A. 1957. Insects affecting seed production in red pine II. *Dioryctria disclusa* (Heinrich), *D. abietella* (D. and S.), and *D. cambiicola* (Dyar) (Lepidoptera: Phycitinae). The Canadian Entomologist, **89**: 70–79. doi:10.4039/Ent8970-2.

MacKay, M.R. 1943. The spruce foliage worm and the spruce cone worm (*Dioryctria* spp., Lepidoptera, Pyralidae). The Canadian Entomologist, **75**: 91–98. doi:10.4039/Ent7591-5.

Martineau, R. 1984. Insects harmful to forest trees. Canadian Forestry Service, Ottawa, Ontario.

McLeod, J.M., and Daviault, L. 1963. Notes on the life history and habits of the spruce cone worm, *Dioryctria reniculella*, (Grt.) (Lepidoptera: Pyralidae). The Canadian Entomologist, **95**: 309–316. doi:10.4039/Ent95309-3.

McLeod, P.J., and Yearian, W.C. 1982. *Dioryctria* coneworm adult activity in a loblolly pine seed orchard in Arkansas (Lepidoptera: Pyralidae). Journal of the Georgia Entomological Society, **17**: 513–517.

McLeod, P.J., and Yearian, W.C. 1983. Ovicidal activity of insecticides on the southern pine coneworm, *Dioryctria amatella* (Lepidoptera: Pyralidae). Journal of the Georgia Entomological Society, **18**: 255–259.

McLeod, P.J., Yearian, W.C., and Young, S.Y. 1982. Effectiveness of *Bacillus thuringiensis* against the southern pine coneworm, *Dioryctria amatella* (Lepidoptera: Pyralidae). Environmental Entomology, **11**: 1305–1306.

McLeod, P.J., Yearian, W.C., and Young, S.Y. 1984. Evaluation of *Bacillus thuringiensis* for coneworm, *Dioryctria* spp. control in southern pine seed orchards (Lepidoptera: Pyralidae). Journal of the Georgia Entomological Society, **19**: 408–413.

Merkel, E.P. 1958. *Dioryctria* cone moth attack as related to cone rush of slash pine in north Florida. Journal of Forestry, **56**: 651.

Merkel, E.P. 1982. Biology of the bald cypress coneworm, *Dioryctria pygmaeella* Ragonot (Lepidoptera: Pyralidae), in north Florida. Journal of the Georgia Entomology Society, **17**: 13–19.

Meyer, W.L., DeBarr, G.L., Berisford, C.W., Barber, L.R., and Roelofs, W.L. 1982. Identification of the sex pheromone of the webbing coneworm moth, *Dioryctria disclusa* (Lepidoptera: Pyralidae). Environmental Entomology, **11**: 986–988.

Meyer, W.L., Cameron, R.S., Tamhankar, A., DeBarr, G.L., Berisford, C.W., and Roelofs, W.L. 1984. Sex pheromone of the blister coneworm moth, *Dioryctria clarioralis* (Lepidoptera: Pyralidae). Environmental Entomology, **13**: 854–858.

Meyer, W.L., Debarr, G.L., Hanula, J.L., Kovalev, B., Cameron, R.S., Berisford, C.W., and Roelofs, W.L. 1986. *Z*-11-hexadecenyl acetate, a sex pheromone component for the southern pine coneworm, *Dioryctria amatella* (Lepidoptera: Pyralidae). Environmental Entomology, **15**: 316–320.

Mihelcic, N., Hanula, J.L., and DeBarr, G.L. 2003. Pathogenic microorganisms associated with the southern pine coneworm (Lepidoptera: Pyralidae) attacking loblolly pine. Florida Entomologist, **86**: 1–7. doi:10.1653/0015-4040(2003)086[0001:PMAWTS]2.0.CO;2.

Millar, J.G., Grant, G.G., McElfresh, J.S., Strong, W.B., Rudolph, C., Stein, J.D., and Moreira, J.A. 2005. (3Z,6Z,9Z,12Z,15Z)-pentacosapentaene, a key pheromone component of the fir coneworm moth, *Dioryctria abietivorella*. Journal of Chemical Ecology, **31**: 1229–1234. PMID:16124244 doi:10.1007/s10886-005-5813-0.

Miller, D.R., Millar, J.G., Grant, G.G., MacDonald, L., and DeBarr, G.L. 2010. (3*Z*,6*Z*,9*Z*,12*Z*,15*Z*)-pentacosapentaene and (9*Z*,11*E*)-tetradecadienyl acetate: attractant lure blend for *Dioryctria ebeli* (Lepidoptera: Pyralidae). Journal of Entomological Science, **45**: 54–57.

Miller, G.E., Hedlin, A.F., and Ruth, D.S. 1984. Damage by two Douglas-fir cone and seed insects: correlation with cone crop size. Journal of the Entomological Society of British Columbia, **81**: 46–50.

Mosseler, A., Roberts, B.A., and Tricco, P. 1992. The effects of fir coneworm, *Dioryctria abietivorella* (Grote) (Lepidoptera, Pyralidae), on seed production in small, isolated populations of red pine, *Pinus resinosa* Ait. Forest Ecology and Management, **53**: 15–27. doi:10.1016/0378-1127(92)90030-D.

Munroe, E. 1959. Canadian species of *Dioryctria* Zeller (Lepidoptera: Pyralidae). The Canadian Entomologist, **91**: 65–72. doi:10.4039/Ent9165-2.

Mutuura, A. 1982. American species of *Dioryctria* (Lepidoptera: Pyralidae). VI. A new species of *Dioryctria* from eastern Canada and north-eastern United States. The Canadian Entomologist, **114**: 1069–1076. doi:10.4039/Ent1141069-11.

Mutuura, A., and Munroe, E. 1972. American species of *Dioryctria* (Lepidoptera: Pyralidae). III. Grouping of species: species of the *auranticella* group, including the Asian species, with the description of a new species. The Canadian Entomologist, **104**: 609–625. doi:10.4039/Ent104609-5.

Mutuura, A., and Munroe, E. 1973. American species of *Dioryctria* (Lepidoptera: Pyralidae). IV. The *schuetzeella* group and the taxonomic status of the spruce cone worm. The Canadian Entomologist, **105**: 653–668. doi:10.4039/Ent105653-4.

Mutuura, A., and Munroe, E. 1974. A new genus related to *Dioryctria* Zeller (Lepidoptera: Pyralidae: Phycitinae), with description of an additional species-group in *Dioryctria*. The Canadian Entomologist, **106**: 937–940. doi:10.4039/Ent106937-9.

Mutuura, A., and Munroe, E. 1979. American species of *Dioryctria* (Lepidoptera: Pyralidae). V. Three new cone-feeding species from the southeastern United States. Journal of the Georgia Entomological Society, **14**: 290–304.

Mutuura, A., Munroe, E., and Ross, D.A. 1969. American species of *Dioryctria* (Lepidoptera: Pyralidae). II. Western Canadian species of the *baumhoferi* and *ponderosae* groups. The Canadian Entomologist, **101**: 1042–1047. doi:10.4039/Ent1011042-10.

Neunzig, H.H. 2003. The moths of North America north of Mexico. Fascicle 15.5. Pyraloidea, Pyralidae (Part). Wedge Entomological Research Foundation, Washington, D.C.

Neunzig, H.H., and Leidy, N.A. 1989. A new species of *Dioryctria* (Lepidoptera: Pyralidae: Phyticinae) from the southeastern United States. Proceedings of the Entomological Society of Washington, **91**: 321–324.

Neunzig, H.H., and Merkel, E.P. 1967. A taxonomic study of the pupae of the genus *Dioryctria* in the southeastern United States (Lepidoptera: Phycitidae). Annals of the Entomological Society of America, **60**: 801–808.

Neunzig, H.H., Cashatt, E.D., and Matuza, G.A. 1964. Observations on the biology of four species of *Dioryctria* in North Carolina (Lepidoptera: Phycitinae). Annals of the Entomological Society of America, **57**: 317–321.

Nicholls, T.H., and Ostry, M.E. 1990. *Sphaeropsis sapinea* cankers on stressed red and jack pines in Minnesota and Wisconsin. Plant Disease, **74**: 54–56. doi:10.1094/PD-74-0054.

Nord, J.C., DeBarr, G.L., Barber, L.R., Weatherby, J.C., and Overgaard, N.A. 1985. Low-volume applications of azinphosmethyl, fenvalerate, and permethrin for control of coneworms (Lepidoptera: Pyralidae) and seed bugs (Hemiptera: Coreidae and Pentatomidae) in southern pine seed orchards. Journal of Economic Entomology, **78**: 445–450.

Pasek, J.E., and Dix, M.E. 1989. Life history of a ponderosa pine coneworm, *Dioryctria auranticella* (Lepidoptera: Pyralidae). Journal of Economic Entomology, **82**: 879–885.

Pedigo, L.P. 1996. Entomology and pest management, 2nd ed. Prentice−Hall, Upper Saddle River, New Jersey.

Phelan, P.L., and Baker, T.C. 1990. Comparative study of courtship in twelve phycitine moths (Lepidoptera: Pyralidae). Journal of Insect Behavior, **3**: 303–326. doi:10.1007/BF01052112.

Prentice, R.M. 1965. Forest Lepidoptera of Canada recorded by the forest insect survey. Volume 4. Microlepidoptera. Department of Forestry of Canada, Ottawa, Ontario.

Ragonot, E.L. 1893. Monographie des Phycitinae et des Galleriinae. *In* Mémoires sur les Lépidoptères. Vol. 7. *By* N. M. Romanoff. M.M. Stassuléwitch, St. Petersburg.

Raizenne, H. 1952. Forest Lepidoptera of southern Ontario and their parasites. Forest Biology Division, Department of Agriculture, Ottawa, Ontario.

Rocchini, L.A., Lewis, K.J., Lindgren, B.S., and Bennett, R.G. 1999. Association of pitch moths (Lepidoptera: Sesiidae and Pyralidae) with rust diseases in a lodgepole pine provenance trial. Canadian Journal of Forest Research, **29**: 1610–1614. doi:10.1139/cjfr-29-10-1610.

Roe, A.D., and Sperling, F.A.H. 2007. Population structure and species boundary delimitation of cryptic *Dioryctria* moths: an integrative approach. Molecular Ecology, **16**: 3617–3633. PMID: 17845435 doi:10.1111/j.1365-294X.2007.03412.x.

Roe, A.D., Stein, J.D., Gillette, N.E., and Sperling, F.A.H. 2006. Identification of *Dioryctria* (Lepidoptera: Pyralidae) in a seed orchard at Chico, California. Annals of the Entomological Society of America, **99**: 433–448. doi:10.1603/0013-8746(2006)99[433:IODLPI]2.0.CO;2.

Roques, A. 1983. Les insectes ravageurs des cônes et graine de conifères en France. Institut National de la Recherche Agronomique, Paris. Pp. 39–55.

Rosenberg, O., and Weslien, J. 2005. Assessment of cone-damaging insects in a Swedish spruce seed orchard and the efficacy of large-scale application of *Bacillus thuringiensis* variety *aizawai* × *kurstaki* against lepidopterans. Journal of Economic Entomology, **98**: 402–408. PMID: 15889731 doi:10.1603/0022-0493-98.2.402.

Ross, D.A., and Evans, D. 1957. Annotated list of forest insects of British Columbia. Part V. *Dioryctria* spp. (Pyralidae). Entomological Society of British Columbia, **53**: 10–11.

Roux-Morabito, G., Gillette, N.E., Roques, A., Dormont, L., Stein, J., and Sperling, F.A.H. 2008. Systematics of the *Dioryctria abietella* species group (Lepidoptera: Pyralidae) based on mitochondrial DNA. Annals of the Entomological Society of America, **101**: 845–859. doi:10.1603/0013-8746(2008)101[845:SOTDAS]2.0.CO;2.

Ruth, D.S. 1980. A guide to insect pests in Douglas-fir seed orchards. Pacific Forest Research Centre, Canadian Forestry Service, Victoria, British Columbia.

Schaber, B.D., and Wood, F.E. 1971. A new species of *Dioryctria* infesting loblolly pine (Lepidoptera: Pyralidae). Proceedings of the Entomological Society of Washington, **73**: 215–223.

Schowalter, T.D., Haverty, M.I., and Koerber, T.W. 1985. Cone and seed insects in Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, seed orchards in the western United States: distribution and relative impact. The Canadian Entomologist, **117**: 1223–1230. doi:10.4039/Ent1171223-10.

Segerer, A.H., and Pröse, H. 1997. *Dioryctria resiniphila* sp.n., eine neue Pyralidae auf *Abies cephalonica* Loud. In Griechenland (Lepidoptera: Pyralidae: Phycitinae). Nachrichtenblatt der Bayerischen Entomologen, **46**: 57–67.

Seifert, M., Wermelinger, B., and Schneider, D. 2000. The effect of spruce cone insects on seed production in Switzerland. Journal of Applied Entomology, **124**: 269–278. doi:10.1046/j.1439-0418.2000.00455.x.

Shea, P.J. 1989. Phytophagous insect complex associated with cones of white fir, *Abies concolor* (Gord. and Glend.) Lindl., and its impact on seed production. The Canadian Entomologist, **121**: 699–708. doi:10.4039/Ent121699-8.

Shea, P.J., Harverty, M.I., and Daterman, G.E. 1986. Impact of insects and methodology for monitoring insects in western pine seed orchards. *In* Proceedings of the 2nd Conference of the Cone and Seed Insects Working Party S2.07-01, Briançon. *Edited by* Alain Roques. Station de zoologie forestière, I.N.R.A.-C.R.F. France, 3–5 September 1986. pp. 147–155.

Shu, S., Grant, G.G., Langevin, D., Lombardo, D.A., and MacDonald, L. 1997. Oviposition and electroantennogram responses of *Dioryctria abietivorella* (Lepidoptera: Pyralidae) elicited by monoterpenes and enantiomers from eastern white pine. Journal of Chemical Ecology, **23**: 35–50. doi:10.1023/B:JOEC.0000006344.18966.c6.

Silvertown, J.W. 1980. The evolutionary ecology of mast seeding in trees. Biological Journal of the Linnean Society, **14**: 235–250. doi:10.1111/j.1095-8312.1980.tb00107.x.

Simonsen, T.J., and Roe, A.D. 2009. Phylogenetic utility and comparative morphology of the composite scale brushes in male phycitine moths (Lepidoptera, Pyralidae). Zoologischer Anzeiger. **248**: 119–136. doi:10.1016/j.jcz.2009.03.002.

Skrzypczyńska, M. 2004. Impact of insects on health of fir *Abies alba* Mill. Seeds exemplified by the Forest District Losie (the Kraków Forest Region). Sylwan, **248**: 29–33.

Sopow, S.L., Bennett, R.G., Landry, J.F., and Landry, B. 1996. Identification of the "grey" *Dioryctria* species of British Columbia (Lepidoptera: Pyralidae). Journal of the Entomological Society of British Columbia, **93**: 75–92.

Speidel, W., and Asselbergs, E.F. 2000. The status of *Ocrisia* Ragonot, 1893, and notes on *Dioryctria*

Zeller, 1846 (Lepidoptera: Pyralidae: Phycitinae). Entomologische Zeitschrift, **110**: 144–146.

Strong, W.B. 2005. *Dioryctria* research in British Columbia. News Bulletin No. 41, Canadian Tree Improvement Association News bulletin. Pp. 2–6.

Strong, W.B., Millar, J.G., Grant, G.G., Moreira, J.A., Chong, J.M., and Rudolph, C. 2008. Optimization of pheromone lure and trap design for monitoring the fir coneworm, *Dioryctria abietivorella*. Entomologia Experimentalis et Applicata, **126**: 67–77.

Trudel, R., Bauce, R., Cabana, J., and Guertin, C. 1995. Rearing technique for *Dioryctria abietivorella* (Lepidoptera: Pyralidae). Journal of Economic Entomology, **88**: 640–643.

Trudel, R., Bauce, E., Cabana, J., and Guertin, C. 1997. Vulnerability of the fir coneworm, *Dioryctria abietivorella* (Grote) (Lepidoptera: Pyralidae), in different larval stages to the HD-1 strain of *Bacillus thuringiensis*. The Canadian Entomologist, **129**: 197–198. doi:10.4039/Ent129197-1.

Trudel, R., Bauce, E., Guertin, C., and Cabana, J. 1999*a*. Diapause induction and overwintering stage in the fir coneworm (Lepidoptera: Pyralidae). The Canadian Entomologist, **131**: 779–786. doi:10.4039/Ent131779-6.

Trudel, R., Bauce, E., Guertin, C., and Cabana, J. 1999*b*. Performance of the fir coneworm *Dioryctria abietivorella* (Grote) as affected by host species and presence or absence of seed cones. Agricultural and Forest Entomology, **1**: 189–194. doi:10.1046/j.1461-9563.1999.00028.x.

Turgeon, J.J., and de Groot, P. 1994. Biology, damage and management of seed orchard pests. Information Report FPM-X-89, Forest Pest Management Institute, Canadian Forest Service, Natural Resources Canada, Sault Ste. Marie, Ontario.

Turgeon, J.J., Roques, A., and de Groot, P. 1994. Insect fauna of coniferous seed cones - diversity, host-plant interactions, and management. Annual Review of Entomology, **39**: 179–212. doi:10.1146/annurev.en.39.010194.001143.

Turgeon, J.J., de Groot, P., and Sweeney, J.D. 2005. Insects of seed cones in eastern Canada. Great Lakes Forestry Centre, Canadian Forest Service, Natural Resources Canada, Sault Ste. Marie, Ontario.

Wang, P.Y., and Sung, S.M. 1982. Description of a new species of *Dioryctria* Zeller on *Pinus sylvestris* var. *mongolica* from north-east China, with establishment of a new species group (Lepidoptera: Pyralidae, Phycitinae). Acta Entomologica Sinica, **25**: 323–327.

Weslien, J. 1999. Biological control of the spruce coneworm *Dioryctria abietella*: spraying with *Bacillus thuringiensis* reduced damage in a seed orchard. Scandinavian Journal of Forest Research, **14**: 127–130. doi:10.1080/02827589950152854.

Witzgall, P., Stelinski, L., Gut, L., and Thomson, D. 2008. Codling moth management and chemical ecology. Annual Review of Entomology, **53**: 503–522. PMID:17877451 doi:10.1146/annurev.ento.53.103106.093323.

Yates, H.O., and Ebel, B.H. 1975. Light-trapping and identifying *Dioryctria* that damage pine cones in northeastern Georgia (Lepidoptera: Phycitinae). Journal of the Georgia Entomology Society, **10**: 76–78.

Zeller, P.C. 1846. Die knotenhornigen Phyciden nach ihren Arten beschrieben. Isis von Oken, **39**: 729–788.

Zobel, B., and Talbert, J. 1984. Applied forest tree improvement. John Wiley & Sons, Inc., New York.