INSECT FAUNA OF CONIFEROUS SEED CONES: Diversity, Host Plant Interactions, and Management

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KEY WORDS: conifers, species richness, feeding guilds, insect-plant interactions, population dynamics, IPM in seed orchards, life-styles, spatio-temporal variations

PERSPECTIVE AND OVERVIEW

Tree reproductive structures—pollen and seed cones, or micro- and megasporangia—represent an extremely rich source of food for many animals (166). Although some species exploit pollen cones (189), in this review we deal exclusively with those exploiting seed cones prior to seed dispersal.

Insects are considered the most important seed predators during the predispersal phase of seed development (59). Previous reviews have examined insect predation on angiosperm seeds and fruits, insect-seed interactions, as well as insect ecology, evolution, and interactions with other animals (86, 166). No general overview of the insects exploiting seed cones of
To meet the increasing demand for forest products, tree-improvement programs were initiated throughout the world during the 1950s (224). Plantations from genetically superior seed were established to satisfy this demand and to help relieve the exploitation pressure on remaining natural forests (185). Foresters fulfilled the initial seed requirements by collecting seed, whenever abundant, from natural stands, seed production areas, or animal caches. Today, many planting programs rely on seed orchards to mass produce seeds that possess high growth rates and desirable aesthetic qualities, as well as resistance to disease, insects, or pollution. Before the initiation of tree-improvement programs, insects exploiting seed cones had received limited attention from entomologists and ecologists; once seed orchards were established, most research focused on seed loss, with little emphasis on ecology.

CONIFER SEED CONES AS A HABITAT

With the exception of the Taxaceae, in which single seeds are surrounded by a fleshy aril, extant conifers bear their ovules in seed cones (96). Most seed cones are located on the adaxial surface of specific categories of shoots and twigs (16, 22, 199) and consist of a main axis bearing spirally arranged bract/fertile ovuliferous scale complexes (12). Each bract associated with an ovuliferous scale, which bears exposed seeds, is joined at the base to the cone axis (12). Because of the diversity of their characteristics (bract, dwarf-shoot, ovules, seed wing, aril) (12, 96), seed cones vary in length (0.2–60 cm), shape, and color (219). Seed cones and seeds represent discrete microhabitats with their own temperature and moisture regime (30, 132, 190) and go through the same photosynthetic process as the rest of the tree (96).

The origin of ovuliferous fructification of conifers cannot be ascertained, although it probably dates back to Palaeozoic times, almost 300 million years ago (12). The diversity of conifers has drastically declined from roughly 10,000 species during the Cretaceous to approximately 600 species today. Only 7 of the 13 currently recognized families of conifers, Araucariaceae, Cephalotaxaceae, Cupressaceae, Pinaceae, Podocarpaceae, Taxaceae, and Taxodiaceae, are still extant (12, 29).

Modern conifers are distributed in both hemispheres with approximately 90% of coniferous forests growing in temperate latitudes (185). They are adapted to mesic and xeric conditions and occupy most ecological niches except extreme desert and tundra.
Reproduction of Conifers

The reproductive cycle of conifers varies, but the overall process is similar: reproductive buds are initiated in the growing season preceding the spring in which seed cones become externally visible; seed cone buds burst open at specific periods to receive pollen, which is carried by wind (219); the time between pollination and fertilization varies from a few days to several months, depending on the type of reproductive cycle (136). Following fertilization, seeds mature and usually disperse immediately or shortly after cones lignify (219); some species do not shed their seeds for several years (16).

The three fundamental types of reproductive cycles vary primarily in the time between reproductive bud initiation and seed maturity (136). In the first type of cycle, which lasts two years, pollination of the seed cone and seed maturation occur during the second year, the year after bud initiation. All Pinaceae except Cedrus spp. and Pinus spp., and a few Cupressaceae, share this cycle. The other two types of reproductive cycle generally last three years, and seed cones mature (increase in size and weight) the year after pollination. The difference between the two types of three-year cycles is based on the time seed cone development stops. For all Cedrus and most Pinus spp. (Pinaceae), Araucariaceae, Podocarpaceae, Cephalotaxaceae, Taxodiaceae, and a few other genera, development stops in midsummer of the second year, shortly after pollination, and fertilization occurs in the third year, shortly after seed cone development resumes. In the second type of three year cycle, which is found in Cupressaceae, fertilization occurs within weeks of pollination and seed cone development continues until the end of the summer of the second year and resumes in the third year.

Compared with the life of the tree, seed cone development is extremely rapid and is characterized by significant morphological and biochemical transformations (96, 141). Roques (161) proposed a pattern to describe the development of seed cones after they burst open consisting of five phases: 1. bud burst (in two-year cycles) or resumption of growth (in three-year cycles); 2. rapid growth, in which macronutrients (N, P, K, Ca, Mg) increase along with sugars and crude fats, and hydrocarbon levels peak; 3. slower growth, in which hydrocarbon content decreases and indigestible fibers, cellulose, hemicellulose, and lignin increase; 4. seed formation and maturation; and 5. cone lignification.

Spatiotemporal Heterogeneity of the Habitat

In natural forests, seed cone production is highly irregular in both space and time. Conifers develop for several years before producing seed cones (219), but once production has begun, it usually continues for the rest of
the tree's life. Cone production usually increases with tree age (22, 199) and continues to increase as long as tree spacing (i.e. crown development) is permitted (22). Nutritional factors, environmental conditions, site characteristics, and altitude also influence cone abundance (78, 96).

For most conifers, large seed crops are synchronized and episodic, a phenomenon referred to as masting (177). Several advantages of this reproductive strategy have been proposed (59, 86, 98, 184). The number of seed cones per tree in mast years varies between species (219). Intervals between mast years, which vary between 2 and 10 years for most species, are characterized by moderate, light, or no cone crops (219).

The spatial distribution of seed cones is heterogenous. The distribution of seed cones usually varies among crown levels. The upper crown, where light is more abundant, generally produces more cones than shaded areas (60, 107, 199, 201). The greatest level of spatial heterogeneity within and between trees, as well as between stands, occurs on edges and during years of poor to moderate crops (161), when production is either limited to a few trees or to a few cones on several trees.

INSECT DIVERSITY AND BIOLOGY

To date, approximately 400 species of phytophagous insects are known to exploit seed cones of world conifers (Table 1). They belong to seven orders: Coleoptera, Diptera, Heteroptera, Homoptera, Hymenoptera, Lepidoptera, and Thysanoptera (e.g. 216); the Lepidoptera have the greatest species richness. Species of the same genera, found in North America and Eurasia, exploit the same resources on congeneric hosts (26, 79, 162, 190).

Taxonomic uncertainties severely hinder the analysis of insect–seed cone relationships. For example, it was recently discovered that damage by Strobilomyia on several hosts on different continents that had been attributed to just a few species is in fact caused by a complex of species (114). Furthermore, 76 entomophagous (218) and several phytophagous insects (26, 79, 154) are still identified only at the genus level or as "near" species. Cytotaxonomic techniques (44) along with variations in isozymes (45) and cuticular hydrocarbons (137) may represent additional tools to address complex taxonomic problems.

About 85% of the insect species are associated with the Pinaceae (Table 1). This proportion is probably biased, as surveys have concentrated primarily on economically important Pinaceae such as Abies, Larix, Picea, Pinus, and Pseudotsuga spp. (47, 119). We could not find studies on insects exploiting seed cones of Cephalotaxaceae, Podocarpaceae, and Taxaceae. Knowledge of the entomofauna of Araucariaceae seed cones is limited (13,
### Table 1 Phytophagous insects exploiting seed cones and seeds of world conifers

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\(^1\)The number following + denotes the number of species added since 1986 (216).

\(^b\)Ar, Araucariaceae; Cu, Cupressaceae; Ta, Taxodiaceae; Pi, Pinaceae.

28, 152) whereas that of Cupressaceae (21, 52, 53, 72, 85, 161) and Taxodiaceae (73, 95, 112, 144) is slightly more extensive.

The insect communities of seed cones are based on the presence of phytophagous insects, which create suitable conditions for the development of mycophagous and saprophagous insects (Chloropidae, Sciaridae, and some Cecidomyiidae and Coleoptera) (79, 161, 179, 181, 182, 186), as well as opportunistic insects that use feeding galleries of phytophagous
insects as hibernating sites (162). The relative importance of each group has been established only for western European conifers (162).

In western Europe, tree species (162), plant introduction (33, 148, 161), and geographical isolation (33) have been shown to influence species richness of seed cone communities. The low number of species known to exploit seed cones probably reflects a stability in the phytophagous insect-cone relationships and a limitation of species diversification to few insect genera that specialize on different structures of the seed cone (161).

Approximately 95% of the 386 natural enemies associated with the seed cone entomofauna (218) are parasitoids; the remainder are predators. Difficulties in collecting and observing predators may explain their limited abundance in observations. Four families of Hymenoptera (Braconidae, Ichneumonidae, Eulophidae, and Pteromalidae) account for over 80% of parasitoids and predators. Parasitoids are extremely polyphagous, suggesting that natural enemies may not be fully adapted to their host (161, 190).

**Guild Structure**

Two broad categories of associations between insects and seed cones have been recognized to date (162, 186). Insects that can feed or develop only in the seed cone (including seeds) are referred to as conophytes. Those that feed or develop in other habitats (foliage, shoots and twigs, cone-bearing shoots and twigs, bark), but that feed or develop on seed cones when these are available, are referred to as heteroconophytes. Usually, congeneric species belong to the same category, except for *Dioryctria* spp., in which some species appear more dependent on seed cones than others (79). In western Europe, more than 71% of the phytophagous insects of indigenous trees are conophytes (162). On introduced trees, however, heteroconophytes are more abundant than conophytes, unless native conophytes were introduced at the same time as the host or the introduced trees are closely related to indigenous hosts (33).

Three patterns of habitat exploitation, or guilds, are commonly recognized (162, 190). *Conophages* feed on cone and bract tissues, usually without damaging the seed directly, although some species may damage seeds. Conversely, *conospermatophages* consume cone and seed tissues, moving from seed to seed in a clear, discriminate pattern. *Spermatophages* develop entirely within seeds; their adaptation to the seed habitat is considered the most specialized (162). Congeneric species usually exploit seed cones in a similar manner and thus belong to the same guild, regardless of the host. In Western Europe, conospermatophages are the most abundant, followed by conophages and spermatophages (162).

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1 Italic indicates a new term we propose.
Bionomics

The life cycles of conophytes are categorized into two groups (162, 186): endoconophytics, which spend their entire preimaginal development (egg to pupa) within the cone, and exoconophytics, which exit the host as a mature larva to pupate elsewhere. In Europe and in North America, the endoconophytic cycle is slightly more common (55–60%) than the exoconophytic (162; JJ Turgeon, unpublished data). Congeneric species have similar life cycles, irrespective of the type of reproductive cycle of the host (161). All spermatophages have an endoconophytic cycle (26, 47, 64, 79, 83, 154, 178, 183, 190, 222). Such cycles are also common among conospermatophages and conophages (25, 26, 53, 79, 105, 154, 169, 212, 220). Most endoconophytic species overwinter as diapausing larvae or pupae within the brood cone or seed (47, 154, 212).

Exoconophytic cycles are common only among conospermatophages and conophages (26, 47, 52, 79, 94, 126, 127, 154, 159, 180, 190, 203, 204, 214). Exoconophytic species overwinter in the duff beneath the tree, mostly as diapausing pupae or mature larvae and rarely as adults (26, 47, 79, 203).

Most heteroconophytes are conophagous lepidopterans that exploit seed cones either because their density is high compared with the volume of foliage provided by the host (161) or because they represent a nutritious food source before vegetative buds burst open and become available as food (140). The life cycles of these insects are more complex and to date no patterns have been recognized, even for species belonging to the same family. Other heteroconophytes include: thrips; homopterans, most of which require two hosts to complete their cycle; heteropterans, which feed alternatively between shoots, needles, buds, and pollen and seed cones; and some coleopterans that destroy seed cones early in development (73, 79, 95, 149, 171, 203, 211).

More detailed information is available on known hosts, geographic distribution, economic importance, morphological description, life history and habits, and type of damage for the most important insects exploiting cones and seeds of conifers from North America (26, 31, 51, 79, 203), Europe (91, 92, 97, 127, 154, 190), northern Africa (52, 53), eastern Asia (21, 25, 55, 72, 84, 95, 195) and the southern hemisphere (13, 28, 225).

INSECT–SEED CONE RELATIONSHIPS

Temporal heterogeneity of seed cone production may well be the most important regulating mechanism in the dynamics of many conophyte populations (106, 159), although the interactions with tree populations are complex and not yet well understood. For example, Mattson (106) suggested
that the early abortion and death of developing seed cones caused by insects may be a positive-feedback process that actually enhances seed cone bud initiation and thus increases the future abundance of resources for insects. Insects adjust to the temporal availability of seed cones at two levels: within seasons to enable insects to synchronize their colonization with seed cone development, and between seasons to ensure availability of resources.

**Relationship with Seasonal Development of Seed Cones**

The relationships between seed cone phenology and the time of colonization by conophytes and heteroconophytes have been established for some species of *Picea* (3, 9, 33, 127, 161, 182, 186, 200, 203), *Abies* (91, 127, 154, 176, 181), *Pseudotsuga* (127, 154), *Larix* (2, 50, 133, 161, 179, 203, 214), *Pinus* (23, 51, 94, 101, 103, 106, 161, 203), and Cupressaceae (52, 53, 161). Such studies have shown that insect colonization occurs during specific, visually recognizable phases of seed cone development (133, 159, 214), which probably reflects an adaptation to the changes occurring within the cone (140, 161). In western Europe, for example, more than 90% of the conophytes colonize phase 2 and 3 of seed cone development, when cones are soft and contain a high level of sugars and a low proportion of indigestible fibers (162). Conversely, more than 85% of the heteroconophytes colonize phase 1 and 4, when cone and foliage tissues are relatively similar in composition (2, 50). The mechanism enabling insects to synchronize colonization with specific phases of seed cone development is poorly understood. While abiotic factors could regulate colonization, for some conophytes, ovarian maturation may be stimulated by the presence of seed cones in the proper developmental stage, thereby assuring synchrony between egg production and suitable oviposition sites (161).

Exoconophytics and heteroconophytes remain in cones until lignification is complete or seeds are released, except for *Strobilomyia* spp. (161). The exit period generally lasts much longer than the colonization period and can be influenced by external cues such as rainfall (3, 143, 161).

**Relationship with Annual Cone Abundance**

Long-term studies have revealed that substantial annual variations in larval populations generally reflect fluctuations in cone abundance (3, 5, 159, 214). The amount of damage variation that can be attributed to cone-abundance variation differs with host species, but generally, an inverse relationship between the proportion of insect-caused damage and change in crop size occurs when an increase in cone abundance outpaces the increase in the insect population and its capacity to attack cones (106, 159, 176, 214).

Most conophyte populations are regulated primarily by larval food availability and may increase substantially with food abundance (106). For
example, the number of cones available per Strobilomyia melania female explained 74–92% of the yearly changes in larval population in the Alps; densities increased only when the current cone crop was two to three times the size of the previous year’s crop (159).

No significant relationships have been established between cone damage by heteroconophytes and annual variation in cone crop (95, 161). Hence, damage by heteroconophytes is often greater than that of conophytes for one to two years following an abrupt decrease in cone abundance (103, 161).

Yearly fluctuations in cone abundance may also play a role in promoting the coexistence of competitively inferior spermatophages with conospermatophages (3). For example, the spermatophages Plemeliella abietina and Megastigmus strobilobius do not appear to be directly regulated by annual fluctuations in crop size as they exploit seeds only during years of heavy to medium crop abundance, which occur after two or three consecutive years of poor cone production have decreased population levels of the conospermatophages (3, 5).

Behavioral Adaptations

Insects have developed several adaptations for coping with spatial and temporal heterogeneity of seed cones and for reducing competition for a limited resource (161). However, such adaptations are not completely effective in maintaining current population levels or in permitting populations to recover quickly, but seem designed mainly to assure survival of some individuals and to prevent extinction in the absence of cones.

While some species offset heterogeneity by exploiting seed cones from a wide variety of hosts (79, 212), others exploit different tree structures of different hosts (42, 198). Dispersal flights to locate cone-producing stands have also been widely reported (87, 161, 170). In addition, some conophyte females adjust oviposition by increasing or decreasing the number of eggs laid per attacked cone when the cone crop decreases or increases, respectively (159), which probably represents a trade-off between the cost of competition and that of not laying eggs. The most common strategy adopted by conophytes attacking conifers with two-year cycles is prolonged diapause, in which insects remain in diapause for more than a year. Parasitoids, and even specialized predators (159), can also undergo a prolonged diapause that is well synchronized with that of their hosts (3, 9, 139, 159, 190).

Prolonged diapause (PD), common among plant-feeding insects dependent on unreliable food supplies (32), could be the result of an evolutionary process related to the appearance of masting in conifers (161). A total of 70 conophytes belonging to the Diptera, Hyme-
noptera, and Lepidoptera can extend their normal winter diapause for one to seven additional years (4, 21, 26, 33, 54, 64, 70, 79, 90, 95, 101, 124, 126, 128, 139, 143, 154, 160, 163, 178, 180, 183, 190, 204, 222, 223; A Roques & JJ Turgeon, unpublished data). PD occurs either in late instars, pupae, or pharate adults. Thus, in any given year, conophyte communities are composed of individuals originating from different cohorts that had been exposed to different conditions of development (161). The significance of this genetic mixing at the population and evolutionary levels is unknown.

In western Europe, 55% of the conophytes, all spermatophages or conospermatophages, are capable of PD (160). The incidence of PD is higher among conophytes exploiting conifers with two-year cycles than with three-year cycles (A Roques & JJ Turgeon, unpublished data). No hypothesis has been formulated to explain this observation. The proportion of individuals from the same species entering PD varies between sites (4, 160).

Different patterns have emerged from results of long-term studies on the relationship between changes in cone production and the incidence of PD (3, 4, 9, 54, 62, 78, 124, 129, 160, 164, 187). In most cases, PD incidence was either inversely correlated with the rate of change in cone yield from the current year to the next (159), or with the size of the cone crop the year following larval feeding (62, 78, 124). However, these correlations generally included a cohort-splitting phenomenon, in which different diapause lengths, including individuals not undergoing PD (161), were observed within each insect generation (159, 164). The incidence and duration of PD may also vary among conspecific insects occupying the same cone (10, 160, 165), different cones on the same tree (160), or different trees in the same stand or orchard (10, 160) but seemed independent of larval densities in seed cones (10). In some Cecidomyiidae, PD incidence was apparently not linked to any of the considered crop variables (3, 124, 187).

Two types of diapause are currently recognized among conophytes (74): risk-spreading and predictive. In the first type, females spread the risk by producing progeny with a mixture of diapause lengths (164). In contrast, species using predictive diapause wait for an environmental cue(s) to terminate diapause the following year (4, 160). Whether PD strategies vary between guilds is unknown, but Hanski (74) has suggested that some conospermatophages exploiting Picea abies use risk-spreading diapause, whereas some of the spermatophages used predictive diapause.

**Diapause initiation** The physiological basis of PD in conophytes as well as the regulating factors of diapause induction are poorly understood. The existence of a genetic polymorphism for PD, involving PD and non-PD morphs, has been speculated (78, 99) but appears unlikely (164). Whereas *Cydia strobilella* individuals that undergo PD can be separated from non-PD
individuals on the basis of their weight (10, 129), those of *Barbara colfaxiana* can be separated on the basis of the degree of pharate adult development and resulting pigmentation pattern, or the dry weight/live weight ratio (165). Such characters can be used to measure accurately the proportion of diapausing insects. Abiotic factors such as temperature (62, 78), rainfall, and solar radiation (160) as well as biotic factors such as host and maternal effects (160, 164) can play a primary role in diapause initiation of some conophytes. The effect of biotic factors on PD induction, however, appears limited to conophytes that exploit seed cones at the time seed cone bud initiation occurs (161).

The chemical composition of seed cones during larval development may also affect PD of some species (124, 160, 164). Such chemicals may provide conophyte larvae with indications of the size, or at least the occurrence, of the future crop or may simply trigger the initiation of PD (124, 160). Preliminary observations of trees treated with hormones to induce seed-cone production revealed a possible role for gibberelins in diapause induction (A Roques, unpublished observations).

The progeny of *Megastigmus spermotrophus* emerging from PD has a significantly higher proportion of non-PD males and females than that of non-PD parents (164). Furthermore, parthenogenic females produce only non-PD males, independent of the PD history of the mother (164), suggesting that fertilization may be necessary for PD induction of males.

**Diapause termination** Predictive PD is probably terminated by the action of abiotic factors because diapausing individuals are either in the litter or in a cone or a seed in the duff. Temperatures occurring during differentiation of seed cone buds in the spring of the year preceding emergence seemed effective in predicting the proportion of *Barbara colfaxiana* that terminated PD (125). Also, cold temperatures during the winter months can terminate PD of *Megastigmus suspectus* var. *pinsapinis* (54). For some conophytes in PD, termination was sometimes positively correlated with the cone production of the host tree (161), whereas for others no relationship could be established over an 11-year period (3, 5).

**Evolutionary Aspects**

The striking similarities in the colonization patterns of conifer seed cones by insects, the exploitation of similar resources by congeneric species, and the relationships between insect attack and cone development have led to the suggestion that the fauna of each conifer may have originated from a common insect that exploited the reproductive structures of the ancestors of conifers (162, 188). Recent studies on intraspecific variations of the cone entomofauna within the range of native trees and the colonization patterns
of introduced conifers by native insects could shed additional light on the evolution of insect–seed cone relationships (33, 162). These results suggest that conophytes were recruited from the heteroconophyte fauna. The dominance of conophytes currently known in certain conifers may, however, limit this recruitment (162), unless the heteroconophytes are highly competitive. Discussions on the evolution or phylogeny of conophytes are scarce and available only for *Megastigmus* spp. (161) and *Strobilomyia* spp. (114).

**HOST SELECTION**

Effective host recognition and selection processes are required, especially by conophytes, to adjust to the spatial distribution of seed cones. For heteroconophytes such as *Choristoneura* spp. and some *Dioryctria* spp., seed cones are selected by larvae capable of moving to find resources (57, 141, 161). For conophytes, females are responsible for seed cone recognition and selection, and the progeny is bound to the female's choice (161; see 79, 128 for exceptions). Furthermore, most conophytes mate either in or on cones (47, 66, 161), or in the vicinity of cones (83, 99, 161, 167), suggesting that cones probably act as rendezvous sites for both sexes.

The two patterns of host detection determined for conophytes are based on adult feeding behavior prior to oviposition (161). When adults feed on seed cones, as is the case of *Conophthorus* spp. and *Pissodes validirostris*, tree rather than cone cues appear to mediate long-range orientation (109, 161). Cone cues may be involved in short-range detection (109) or determination of host suitability (198). On the other hand, adults feeding on flowers or honeydew (158, 167) apparently use both tree and cone cues for long-range orientation. Once within the tree crown, these adults rely heavily on cone cues to locate cones (66, 158, 167) and assess their suitability. The cues used by nonfeeding adults, such as cecidomyiids, *Cydia* spp., or *Dioryctria* spp., are unknown, although these insects probably behave similarly to those feeding on flowers.

Visual and chemical stimuli, operating sequentially or simultaneously, play a role in host location by conophytes. The response of insects to cues provided by cones may vary among sexes (66) and can be influenced by the reproductive (24, 156) and nutritional status of the individual (66).

**Visual Cues**

A recent review of the importance of visual cues in the host-selection process of conophytes indicated that tree silhouette, size and shape, cone size, shape and color and contrast between foliage and cone color can assist conophytes in the recognition and selection of host trees (202).

Spectral patterns of trees, reviewed by Prokopy & Owens (142), provide
only limited species-specific information for cone insects (158, 161). A wide range of conifers have remarkably consistent foliage reflectance, peaking at ~550 nm, because of the absorption properties of chlorophyll. Cone reflectance of conifers with two- and three-year cycles differ. Most seed cones developing on conifers with three-year cycles are green and present a spectral reflectance similar to that of foliage. On the other hand, the cone color of most conifers with two-year cycles differs from that of foliage, mostly because of anthocyanine pigments. For such cones, reflectance generally peaks at ~630 nm, though intraspecific variations in cone color occur (161). The resulting cone-foliage contrast, as estimated from the ratio of cone and foliage relative reflectance, peaks within the green-yellow (520–560 nm) range (158). This reflecting contrast is not specific in wavelength but appears to differ in absolute value between species. Insects might use the absolute value of the ratio to differentiate tree species (202).

The cone-foliage contrast only varies slightly during seed cone development, so it is unlikely to provide cues on seed cone developmental phases needed for the selection of appropriate oviposition sites (156).

INSECT RESPONSE Knowledge of the spectral sensitivity of conophytes is limited to electrophysiological responses of *Strobilomyia melania* to pure wavelengths (161). Its sensitivity extends from ~350–650 nm with two peaks: the major at ~542 nm, the same as the foliage peak, and the minor at ~487 nm, in the blue-green range. Spectral sensitivity above 600 nm, where cone reflectance peaks, is weak (161).

The visual cues used by conophytes that feed on nonhost plants (e.g. flowers) usually change during the host-detection process (161), partly influenced by the adult's nutritional and reproductive status. For example, unfed adults of *Megastigmus* spp. were attracted primarily to yellow designs that mimic flowers, whereas satiated adults shifted to the green colors that represented conifer host patterns (66, 158). The preference for the green color lasted up to 36 hours, after which time, yellow once again became attractive (66). Furthermore, tests with *S. melania* revealed that flower-type yellow surfaces were mostly attractive to sexually immature adults, whereas surfaces providing ovipositional cues were attractive to mature flies (156). Blue, cone-mimicking traps hung within the canopy attracted primarily (>90%) females that were not ready to oviposit (24).

The contrast between cone and foliage color probably acts as a stimulus for adults in search of mating and oviposition sites within a stand (156). Vertical surfaces that mimic and intensify the natural cone-foliage reflectance contrast [e.g. a fluorescent yellow surface with purple stripes (89)] elicited the arrival from a distance of mature *S. melania* when placed in front (~1 m) of cone-producing trees (156). Alightment on this type of trap was
negatively correlated with the percent UV and blue reflectance and positively correlated with the percent green-yellow reflectance (156). However, alightment on such traps differed among Strobilomyia spp. (202, 214) and the sex ratio was heavily biased, with traps catching 3–20 times more S. melania males than females (89, 156). These differences suggest either distinct species- and sex-specific requirements of hue, saturation, and intensity or different foraging behaviors (202).

Tests with cone-mimicking lures hung within tree canopies confirmed that Strobilomyia spp. used cone color to locate hosts from nearby or within the canopy (24; J Turgeon & A Roques, unpublished observations). Alightment on such lures was positively correlated with the percent blue reflectance and negatively correlated with the percent UV and green reflectance (24). Seed cones also provide some visual cues to Megastigmus spp. (158), as evidenced by their attraction to berry-like green lures during their search for mating and ovipositing sites (66). Yellow surfaces placed near cones in the canopy represent the most effective lure for several species of Megastigmus (90, 130, 167). Cone color, or cone-foliage contrast, may also play a role in host detection by some Coleoptera. The proportion of Pinus monticola green cones destroyed by Conophthorus ponderosae was significantly lower than that of purple cones, but only when cone abundance was moderate or low (88).

Different visual cues appear to play a role in conifers without cone-foliage contrast. Tree silhouette is likely involved in host detection by Conophthorus spp., as damage was higher in stands that maximize silhouette perception (88, 109). Furthermore, both sexes of P. validirostris oriented almost exclusively to colors with a reflectance pattern roughly similar to that of pine bark—black and reddish brown (161).

Shape and dimension of cones may also play a role in the close-range host-detection process. For example, M. bipunctatus can discriminate various shapes, preferring rhomboids over six other shapes (66). P. validirostris also orient towards vertically elongated shapes resembling cone-bearing pine leaders (161). Mattson (108) suggested that the attack and cone-handling behavior of Conophthorus spp. has evolved in relation to the size of the cones of its pine species. Variation in tree or clonal susceptibility to insects is sometimes related to cone length and diameter (99, 147, 148); however, these studies used final cone size, or cone size four weeks after oviposition, rather than cone size at the time of oviposition. Whether cone length at maturity is related to cone length at oviposition was not established. The influence of cone dimensions or shape in the long-range detection appears more limited. Various m in front of trees caught fewer S. melania flies than those with the cone-foliage contrast (158).
While the visual attributes of seed cones provide a search image for some insects when the cones clearly contrast with foliage (158), probably more specific cues are used to locate seed cones at the right phenological phase.

**Olfactory Cues**

The involvement of cone volatiles in long- and short-range (trees with cones and seed cones, respectively) host-selection process of conophytes has been suspected for some time. Little work, however, has been done to demonstrate differences in volatile emissions that could allow conophytes to distinguish seed cones of different species; seed cones from foliage, twigs, or shoots; and seed cones at various stages of development.

Numbers of cone volatiles, mostly terpenoids with some aliphatic alcohols and esters, differ among conifers; 17 compounds for *Picea abies*, 12 for *Larix sibirica*, and 9 for *Pinus sylvestris* (14). The monoterpane profiles of *Pseudotsuga menziesii* and *Larix decidua* also vary significantly between cones, but not among cones and among ramets from the same clone (146).

Volatile emissions of cones differed markedly from those of foliage and twigs, although within-tree variability can be large for some species (109). Although *P. abies* cones emitted terpinolene and 10 aliphatic alcohols and esters that are not found in twigs (14), cones and foliage of *P. menziesii* and *L. decidua* differed mainly in the amount of monoterpenes emitted (146). When monoterpane profiles of cones, shoots, and needles are similar, as is the case for *Pinus resinosa*, oleoresins can have different sesquiterpene profiles (109).

Differences between the terpenoid profiles of bract and scale oleoresins extracted from the same cone, an indication of within-cone variation in volatiles, have been reported for *P. menziesii* and *L. decidua*. Whether within-cone variations in volatiles can be used by insects such as *S. melania*, which oviposits at the junction of bracts and scales (161), remains to be determined.

Volatile emissions from *L. decidua* and *P. menziesii* cones at distinct phenological phases also differ (146). Differences in the terpenoid spectrum of cone oleoresins of cones at different stages of cone development have also been reported (135), suggesting that cone volatiles probably provide the specific cues used by conophytes for oviposition.

Qualitative and quantitative modifications of the cone volatiles occur after insect attack. Cones of *L. decidua* attacked by *Strobilomyia laricicola* and *S. melania* had higher levels of β-phellandrene and limonene than undamaged cones (146), and major monoterpenes of cone oleoresins changed after cone colonization by *P. validirostris* and *Strobilomyia anthracina* (135, 194). Such changes probably either attract or repel other insects (135), and they might act as an oviposition-deterring pheromone (ODP). As yet no
chemical evidence indicates that any of the conophytes produce ODPs to reduce competition, although the spatial distribution of eggs supports this hypothesis for some species (123, 159).

**INSECT RESPONSE** The response of conophytes to cone volatiles is extremely variable among species (1, 43, 76, 104, 135, 161) and may (1, 158) or may not (135) differ between sexes. Results differ with the testing procedures (cone extracts vs specific compounds), and knowledge about the roles played (long- or short-range orientation, repulsion) by the specific compounds tested is lacking. Furthermore, knowledge of the sensory systems involved in the long- and short-range detection of the chemical cues provided by trees and seed cones, and their suitability as oviposition sites or feeding sites, is limited (66, 161, 167).

The response of some conophytes to cone volatiles may also be affected by the insects' nutritional and reproductive status. For example, adults of *Megastigmus bipunctatus* fly toward extracts of *Juniperus* sp. berries only when fed (66). While sexually immature females did not respond to seed cone volatiles, mature females of *S. melania* and *Megastigmus spermotrophus* discriminated between pentane extracts of seed cones at various stages of development, preferring the stage on which oviposition takes place (158).

The degree of colonization by some conophytes may be influenced by the levels of volatile emitted by cones or foliage at the time of attack. For example, a positive relationship has been established between the levels of myrcene, 3 carene, β-phellandrene, and p-cymene in the oleoresin of *Pinus sylvestris* needles and the proportion of cones attacked by *P. validirostris* (7). Also, the level of limonene, myrcene, and terpinolene in *P. menziesii* seed cones has been positively correlated with the intensity of *M. spermotrophus* colonization (146).

It is still unknown whether conophytes can use the variation in quality and quantity of the chemical messages provided by the tree or the seed cones, and at which point in the plant-selection process they use volatiles. A typical conifer forest is so rich in volatile compounds that insects could be oblivious to olfactory discrimination of tree species until they were ready to land (109), but increasing evidence suggests that several conophytes rely on a combination of visual and olfactory cues in long- and short-range cone finding (89, 109, 161).

**Precision of Host Selection**

Often, female host preference and host suitability for larval development are positively correlated, although host selection is unlikely to be totally precise (57, 109). Evidence that host selection is not a fail-safe process has
been reported for several conophytes (99, 161, 167, 198). For other species, the host-selection process is not as developed or precise as originally believed. For example, *M. spermotrophus* was considered capable of selecting fertilized *P. menziesii* ovules as oviposition sites in pollinated seed cones (4, 83, 167). However, *M. spermotrophus* oviposition precedes ovule fertilization in most years (161), and recent experiments have clearly demonstrated that females oviposit, and larvae develop, in unfertilized seeds of unpollinated seed cones (130, 147, 161). How unfertilized seeds support the entire development of a chalcid larva is still unclear, although *Megastigmus* spp. might all be gall makers (147), and as such probably modify the growth of unfertilized seed.

**PEST MANAGEMENT IN SEED ORCHARDS**

In the early 1950s, the desire for genetically superior tree seed of known quality and parentage for reforestation programs led to the establishment of seed orchards to produce maximum amounts of genetically improved seed as quickly, reliably, and efficiently as possible (224). The high value of seed and the great amount of capital and operating funds needed to establish and maintain high seed outputs result in low tolerance for cone and seed damage.

Generally, seed orchards are small (often less than 20 ha), even-aged plantations consisting of a single species represented by a few genetic families or clones artificially selected for commercially desirable traits. Trees are planted in regular and widely spaced rows. Orchards are usually established on flat or gently sloping sites with average soil fertility and good air circulation and are isolated to reduce pollination from outside sources (224). In many orchards, a grass cover protects the soil from erosion and compaction and facilitates the movement of tractors and other heavy equipment. These management practices are fixed, because they cannot be changed or manipulated after the seed orchard has been established. On the other hand, other practices such as fertilization or hormonal treatments, girdling, tree removal to increase spacing, or top and root pruning may be implemented several times throughout the life of the orchard to produce frequent, abundant, and easily harvestable crops of viable seeds. These management practices have greatly altered the population dynamics of the cone crop (161), and thus the insects. Because the temporal and spatial fluctuations in cone abundance typical of natural stands are gone, pest-management programs must operate within the constraints imposed by these practices. An integrated approach to pest management in seed orchards must include ecological information on host and pests, methods to predict crop and pest abundance and their impact, and management options.
Assessment of Pest Abundance and Impact on Seed Crop

Cone crop (cohort) life tables have been used extensively in orchards to assess the relative impact of abiotic and biotic mortality factors (36, 56, 93, 100, 150, 174). They have been combined with mortality analyses of seeds to produce operational cone-inventory or cone-crop monitoring systems (15, 46, 48, 58, 80, 81, 154). Furthermore, these systems can be used at the clonal or family level, or for the entire orchard, to: (a) estimate and predict cone and seed crop size at various times, (b) identify good and poor cone producers, (c) identify the pest(s) causing damage and estimate its current and potential damage, (d) provide a cost analysis of seed production, and (e) estimate the efficacy of pest-management treatments, among other factors (46).

To complement crop-monitoring systems, simple and expedient insect sampling and monitoring techniques are required to predict more accurately seed loss before serious damage is done (157, 197) and to time control measures and assess their efficacy (18). For example, sequential sampling methods that classify egg densities as either above or below a critical density have been developed (120, 196). Egg sampling, at specific stages of cone development, is probably the most accurate method of predicting seed loss of conophytes, chiefly because it reflects insect immigration and emigration in the orchard and eliminates the need to calculate the proportion of insects that either remained in prolonged diapause or exited. However, alternate methods of assessing population densities or predicting damage have had to be developed because the time frame available is usually short, the process is extremely labor intensive, and the eggs of some conophytes such as Megastigmus spp. are extremely difficult to detect.

Black light traps were used to monitor the flights of several species such as Dioryctria spp. in southern pine seed orchards (217), but they lacked species specificity and have been largely replaced by sex pheromone traps. These traps are easy to use, economical, versatile, usually effective at low insect populations, and are frequently used to detect adult populations or to monitor the initiation, duration, and magnitude of their flight periods (38, 39, 67, 209). Many factors that contribute to the success of a pheromone-based monitoring program have been examined, including: rate, uniformity, and duration of pheromone release; cross attraction and inhibition responses of the moths; moth migratory behavior; and trap location, trap design, and trap density (38, 39, 67–69, 75, 77). Research on the traps' usefulness, reliability, and accuracy in predicting cone or seed loss has, however, received much less attention. Trap-catch thresholds to indicate when insecticide applications are needed have been established only for
some Dioryctria spp. (209). This knowledge gap probably stems from the inability of the pheromone traps to provide estimates on the origin, location, and density of egg-laying females (111). Problems, limitations, progress, and future research needs associated with the use of sex pheromone and other semiochemicals to manage pests of conifer seed orchards have been reviewed elsewhere in more detail (39, 67).

Alternatively, traps that mimic visual cues used by some conophytes to locate cone-producing trees or seed cones currently serve to predict the beginning of emergence, the relative abundance of the species present in specific stands, and the potential damage of Strobilomyia spp. (157, 202). However, such traps often attract other species of flies that are morphologically similar. When this occurs, time-consuming separation of species by examination of the genitalia is required to accurately determine trap catch. Whether the use of visual traps baited with host volatiles, or strictly host-volatile traps, may increase trap specificity is currently being investigated for several species (146).

Economic analysis of the amount of damage that can be tolerated in orchards before pest management is justified have seldom been done (41, 117). Instead, managers often set an arbitrary injury level (35, 47), usually near zero (17) or 10% (121, 196). Realistic and stochastic economic injury levels and thresholds (138) have not been developed for any of the major cone and seed insects; these will be needed if integrated pest management (IPM) is to be implemented (41, 208).

Management Options

The first practical control methods developed, and those that continue to dominate in seed orchards, depended on chemical insecticides. Detailed ecological studies needed to implement biological or cultural tactics against insects destroying entire cone crops (26, 79, 97, 154, 190, 203) are unavailable.

Contact insecticides are sprayed directly onto foliage either by ground or aerial application equipment (35, 115). During the past 30 years, several contact insecticides have been tested and registered for use; of these, azinphosmethyl has been the most commonly and longest used (35). More recently, the synthetic pyrethroids, esfenvalerate, fenvalerate, and permethrin, have been used in North America and Europe (6, 19, 131, 193, 206). Systemic insecticides that are translocated within the tree to the cones' interior control conophages and conospermatophages (37, 191, 206), but are not always effective in controlling spermatophages (2, 113), probably because the amount of insecticide translocated to seeds is minimal. Systemics are applied to the tree by trunk injection, implantation, foliar application,
or soil application (63, 113, 151, 191, 206). Dimethoate has been used frequently throughout much of the world (6, 47, 49, 100, 134, 192).

Seed orchard managers have philosophically embraced integrated pest management (e.g. 34, 101), but how IPM is conceptualized varies within and among regions of the world. In some regions, IPM is seen as an ecological strategy that relies first on natural enemies and constraints of the ecosystem, and secondly on direct intervention. In other regions, IPM is a strategy that combines all suitable direct and indirect techniques to maintain populations below a desired economic threshold.

IPM in seed orchards is in its infancy (71, 138). The high cost of acquiring ecological data for an effective IPM system has mitigated efforts to abandon chemical insecticides, which are effective, well-established, relatively inexpensive in the short term, psychologically satisfying to the user, and require minimal biological data.

Insecticide resistance and secondary pests, two of the strongest pragmatic reasons to move from routine insecticide applications to IPM, have not been a serious problem in seed orchards. The lack of insecticide resistance can probably be attributed to the rapid reinvasion of the orchards by susceptible members of the target species and by their natural enemies from the surrounding untreated natural forests. Nevertheless, the recent occurrence of secondary or induced pests caused by the application of synthetic pyrethroids (e.g. 27, 145) compels a reconsideration of pesticide use. Policies that restrict the application of chemicals, as well as deregistration, also affect the future of chemical control (19, 41).

Several factors delay the implementation of IPM (208), but the most serious in seed orchards is probably the lack of effective and cost-efficient biological or cultural pest control methods, which must provide a high level of protection because of the low economic injury levels. Nonetheless, the constraints to IPM in seed orchards are being overcome and progress is being made to identify and develop more ecologically based tactics. For example, mating-disruption experiments that exploit pheromone-mediated mating behavior have been on-going in the southeastern United States since 1980 (38, 39, 67). The low population density of many of the cone and seed insects in orchards enhances the efficacy of the mating-disruption technique, but the lack of orchard isolation from natural stands may limit the effectiveness of this tactic. Mass trapping of cone and seed insects has not been undertaken, but might be used to clean up populations, or to supplement other control tactics that are less effective at low populations (67).

As an alternative to pheromones, traps that mimic visual cues, either alone or in combination with olfactory cues, have considerable potential for
reducing populations. Recently, Gao et al (65) demonstrated in Chinese seed orchards that 60 yellow sticky traps/ha captured enough Strobilomyia adults to decrease seed damage. Active research programs on other Strobilomyia spp. in Europe, Canada, and China seek to further develop this tactic. Also, clear sticky bands applied around the bole have effectively reduced damage by the flightless weevil Lepesoma lecontei (175).

Biological control with macroorganisms also offers some interesting possibilities. Preliminary studies with Scambus punctatus, an ichneumonid, indicates that mass release of this parasitoid may control P. validirostris in China (221). Although attempts to control Barbara colfaxiana with the egg parasitoid Trichogramma minutum were unsuccessful (82), tests are planned for other possible hosts.

The microbial insecticide Bacillus thuringiensis (Bt) has been in experimental use in seed orchards since the mid-1970s. Because its efficacy is typically lower than that of pesticides (e.g. 20, 102, 110), it has not replaced chemical insecticides in operational control programs, although it is registered in the US for the control of Dioryctria spp. The only other tested microbial insecticide is Beauveria bassiana, a general fungal pathogen. It has shown promising, but inconsistent, results in the control of Strobilomyia spp. exploiting Larix spp. (205) and Picea spp. (61); its use has not advanced beyond the experimental stage.

Seed orchard or crop management practices that markedly influence insect densities have also been identified and are used either to hinder population increases or to focus management actions. For example, insect densities in seed orchards are often higher than in surrounding stands, which serve as reservoirs (161, 173). Moreover, some clones of several species of Pinaceae are more susceptible to insect damage than others (7, 8, 88, 161, 172). Thus, knowledge of insect distribution or of clonal variations in susceptibility to insects, which are often less obvious when cones are extremely abundant (88, 161), can be used to concentrate pest management efforts where wanted or needed (34).

The removal of colonized cones at harvest is another effective method to reduce conophyte populations residing within the orchard. For example, this method effectively reduced the population of Sinorsillus piliferus, which overwinters as a nymph in the cones (73). Alternatively, infested cones may be destroyed within the orchard. In the US, burning the infested cones that have fallen to the ground has proven effective for control of Conophthorus coniperda (207). The removal of cones may not prevent population increases of all pests, as some species invade the orchards from surrounding stands (87, 161). Consequently, the removal of host trees from within a radius of several kilometers of an orchard, combined with the annual removal
of all cones, may limit the impact of *Megastigmus spermotrophus* (161). This approach is currently under further evaluation for this species.

The misting of cones with cold water to reduce pollen contamination from nearby stands can also substantially reduce damage by *Contarinia oregonensis* (116). Also, when seed production in orchards reaches its peak, the supply of seed may exceed the demand and surplus seeds can be stored. Pest management can then be suspended until the surplus is depleted. Managers could optimize this strategy by using insect control only when large crops are anticipated. For example, in North Carolina, *C. coniperda* was controlled by a prescribed burning program through the orchard the year before the maturation of the largest cone crop of *P. strobus* in 30 years. This strategy produced enough seed for at least 10 years, during which time no further control of the cone beetle will be required (G DeBarr, personal communication). Seed orchard managers may also occasionally consider the abortion of a cone crop to allow the trees to rest and produce more vegetative growth. Cone abortion, timed to occur during a vulnerable stage in the insect's life cycle, could be another effective method of cultural control.

**CONCLUDING REMARKS**

Our knowledge of the entomofauna of conifer seed cones comes primarily from the pest species of Pinaceae. Such information may not reflect the host-insect relationships of other conifer families, but it certainly provides a framework to formulate working hypotheses for associations and for colonization and exploitation patterns of conifers that have not been studied, or for which the entomofauna is not fully known. Furthermore, because of the characteristics of the habitat, this model system could contribute greatly to the understanding of the effect of temporal and spatial variation of resources on animal-plant interactions and of its implication for pest management. Finally, in our view, IPM will succeed as an operational practice when seed production is viewed as an optimization rather than a maximization process and when it is based on an ecological and evolutionary framework.

**Acknowledgments**

We thank A Battisti, GL DeBarr, GG Grant, WJ Mattson, JN McNeil, N Rappaport, TD Schowalter, M Skrzypczyńska, JD Sweeney, and H Zwölfer for helpful comments and suggestions on an earlier version of this manuscript and C Plexman and R Burgess for their suggestions on terminology of Greek origin.
Literature Cited


in Douglas-fir seed orchard in Western Oregon. *J. Econ. Entomol.* 81:281-85.


62. Fogal WH. 1990. White spruce cone crops in relation to seed yields, cone insect damage, and seed moth populations. See Ref. 210, pp. 76-88.


73. Han MD, Peng JW, Pan SS. 1993. Control of Chinese fir seed bugs in Hunan province. See Ref. 40, In press
88. Jenkins MJ. 1983. Relationship between attacks by the mountain pine cone beetle (Coleoptera: Scolytidae) to clone and colour in Western white pine. Environ. Entomol. 12:1289–92
90. Jensen TS. 1993. Diapause and phenology of the seed chalcid Megastigmus pinus and the infection of Abies procera cones in Denmark. See Ref. 40, In press
INSECTS OF CONIFER SEED CONES


118. Deleted in proof


134. Olenici N. 1993. Stem injection of dimethoate for control of European larch (Larix decidua) cone and seed insects. See Ref. 40, In press


171. Schowalter TD. 1986. *Lepesoma...*
lecontei (Coleoptera: Curculionidae): an agent of conelet abortion in a Douglas-fir seed orchard in western Oregon. J. Econ. Entomol. 79:843–46

172. Schowalter TD, Haverty MJ. 1989. Influence of host genotype on Douglas-fir seed losses to Contarinia or- egonensis (Diptera: Cecidomyiidae) and Megastigmus spermotrophus (Hymenoptera: Torymidae) in western Or­ egon. Environ. Entomol. 18:94–97


175. Sexton JM, Schowalter T. 1991. Physical barriers to reduce damage by Lepesoma lecontei (Coleoptera: Curcu­ lionidae) to conelets in a Douglas-fir seed orchard in western Oregon. J. Econ. Entomol. 84:212–14


178. Skrzypczyńska M. 1975. Eurytoma bouceki n. sp. (Hymenoptera, Eu­ rytomidae), its stages of development, biology and economic importance. Z. Angew. Entomol. 79:204–13


182. Swrzychyńska M. 1982. The ent­ omofauna of the cones of spruce, Picea abies (L.) Karst. in Poland. Z. Angew. Entomol. 94:21–31


188. Stadnitskiy GW. 1986. The role of plant reproductive structure in land insects origin. See Ref. 155, pp. 179–82


196. Sweeney JD, Miller GE. 1989. Dis­ tribution of Barbara colfaxiana (Kearfott) (Lepidoptera: Tortricidae) eggs within and among Douglas-fir
crows and methods for estimating egg densities. *Can. Entomol.* 121:569–78

197. Sweeney JD, Miller GE, Ruth DS. 1990. Sampling seed and cone insects in spruce. See Ref. 210, pp. 63–75


211. Williams VG, Goyer RA. 1980. Comparison of damage by each life stage of *Leptoglossus corculus* and *Tetysa bipunctata* to loblolly pine seeds. *J. Econ. Entomol.* 73:497–501


punctatus: a preliminary report. See Ref. 40, In press


