Bark and Wood Boring Insects in Living Trees in Europe, a Synthesis

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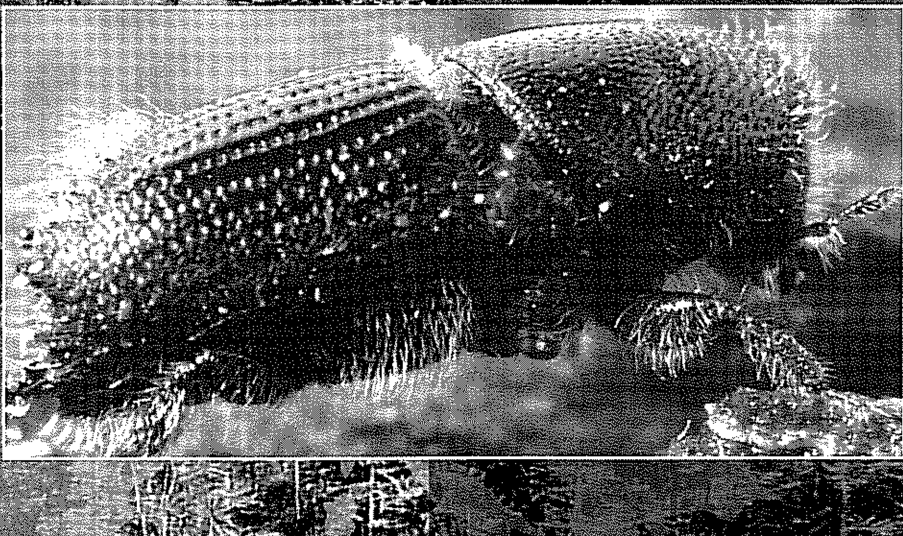

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Ips sexdentatus (six-spined engraver beetle), a bark beetle attacking pines (photo taken by Janin – INRA).

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Chapter 17

FUNGI ASSOCIATED WITH *HYLOBIUS ABIETIS* AND OTHER WEEVILS

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1. INTRODUCTION

Many weevils (Coleoptera: Curculionidae) carry fungal spores to their host trees. According to Leach (1940), an insect can be considered to be a vector if it 1) is consistently associated with an infected plant in the field, 2) visits healthy host plants under conditions when infection is possible, 3) carries pathogen inoculum with it in the field, and 4) is able to transmit the pathogen to a healthy plant under controlled conditions. Most of the well-known weevil-fungus associations are from North American species carrying root-rot or staining fungi. The association of European weevils with fungi has so far not been reviewed extensively, and research focused solely on transmission of fungi is scarce. In many cases associations between weevils and fungi have been found as extra information in investigations set up to study different topics, e.g. spread of the pathogenic root-rot fungus *Heterobasidion annosum coll.* (Fr.) Bref.

In weevils, association with fungi is closely connected with the phloephagous feeding guild, which involves feeding on the fresh, highly nutritive phloem and inner bark. The weevils that make large patches of feeding scars with their chewing mouthparts are the possible inoculum agents of harmful fungi. During their emergence from pupal chambers and galleries, most weevils are contaminated both internally and externally with fungal spores.

Generally, for transmitting fungi, bark beetles are more important than weevils (Whitney 1982; Harrington 1988; Beaver 1989). Very few true Curculionidae have developed a mutualistic association with fungi (Bright 1993). Consequently, none of the weevils have mycangia or similar structures for transporting fungi. This suggests that primitive Curculionidae did not require fungi to aid in host discovery and utilisation and thus followed a different evolutionary pathway (Bright 1993). The most harmful European weevil, the large pine weevil *Hylobius abietis* L., feeds on seedlings but breeds mainly in stumps and roots. Overall, it is questionable whether

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there are any direct benefits for large pine weevil about fungal associates, as they compete for the same resources.

Disparate genera of ophiostomatoid fungi have evolved similar structures as adaptations to insect dispersal. From the standpoint of fungi, reliable spore dispersal and inoculation to a suitable habitat are crucial. Further, direct penetration through the cell walls is an effective method of dispersal. Most fungi associated with European weevils seem to be only slightly or moderately pathogenic and are introduced to stressed trees. Among the few exceptions are the highly pathogenic *H. annosum* (Jørgensen and Beier Petersen 1951; Laine 1977) and the causal agent of resin-top disease *Peridermium pini* (Pers.) Lév (Pappinen and von Weissenberg 1994a, b, 1996). The prevalence of insects and fungi varies, and in European weevils it seems that the opportunity for contact with pathogenic fungi is occasional and occurs when population density is high.

In Europe the number of pathogenic weevil-disseminated root diseases in pole-size and mature conifers is lower than in North America. It appears that the root-collar zone, used *e.g.* by *Hylobius warreni* Wood (Cerezke 1994) and *Hylobius pinicola* (Couper) in the boreal forest in Canada, seem to be used less effectively in Europe than in North America. The unique type of wilting disease, black-stain root disease, spread by root-feeding insects and caused by the fungus *Leptographium wageneri* (Kendrick) Wingfield has limited occurrence in Europe compared to Western North America where the disease commonly occurs (Morelet 1986). Further, in the genus *Hylobius* there are seven species in North America, whereas in Europe there are only four species, of which only three live on conifers. In Europe, we have no harmful species of the genus *Steremnius* or *Pachylobius*. Nevertheless, among the European curculionids there are some potential fungal vector candidates (Table 1).

2. BLUE-STAIN FUNGI ASSOCIATED WITH EUROPEAN WEEVILS

2.1. Hylobius abietis

Species of *Leptographium* are anamorphs of *Ophiostoma* H. & P. Sydow (Ascomycetes). Although some of these species are associated with transmission by specific bark beetles, most of them are associated with a broad group of bark beetles and curculionids. *Leptographium procerum* (W.B. Kendr.) Wingf. is known to be distributed worldwide, mostly in pines and spruce. It has been isolated *e.g.* from Canada, Croatia, England, Finland, France, New Zealand, Norway, Poland, South Africa, Sweden, and the USA (Kendrick 1962; Hallaksela 1977; Halambek 1976; Jacobs and Wingfield 2001). The fungus, when inoculated into two-year-old *Pinus strobus* L. seedlings, caused mortality (Halambek 1976).

In Europe, the fungus does not have a well-recognized insect vector; but both sexes of the large pine weevil have been found to carry *L. procerum* (Lévieux *et al.* 1994a). Fungal spores are located on the dorsal and lateral sides of the pronotum, especially anteriorly. Sticky masses of spores are situated in cuticular depressions associated with the pronotal setae. According to Piou (1993), 3-47% of the emerging large pine weevils and 18 % of the seedlings killed by pine weevil were infected with *L. procerum*. In addition, in France the staining fungi *Leptographium wingfieldii* Morelet (7%), *Ophiostoma canum* (Münch) H. & P. Sydow (2%) and *O. piliferum* (Fries) H. & P. Sydow (1-3%) have been detected in low frequencies on emerging pine weevils (Piou 1993). Furthermore, *Leptographium alethinum* Jacobs, Wingf. & Uzunovic has been isolated from the galleries of the pine weevil in England and Scotland. This species has recently been distinguished from *L. procerum* by the absence of rhizoids (Jacobs *et al.* 2001). The pathogenicity, distribution and overall significance of *L. alethinum* or the other possible stain-fungi associates of pine weevil are not known. The structural variation of the conidiophores, however, suggests the presence of various fungi (Lévieux 1994a).

2.2. Pissodes weevils

In France, about 10 % of the *Pissodes piceae* Illiger individuals carry *O. canum* and *O. ips* (Rumb.) Nannf., indicating a low rate of infestation on fir (Lévieux 1994b). The largest patches of spores were located on the sides of the pronotum and sometimes on the elytra and rostrum. *Ophiostoma minus* (Hedgcock) H. & P. Sydow, *Ophiostoma pini*, *Ceratocystiopsis minuta* (Siem.) Upad. Kendrick, *O. piceae* (Münch) H. & P. Sydow, *O. pluriannulata* (Hedgcock) H. & P. Sydow, *O. stenoceras* (Robak) Melin & Nannf. and *Aureobasidium pullulans* (de Bary) Arnaud have sometimes been found associated with *Pissodes pini* L. (Mathiesen-Käärik 1953, 1960). *O. minus* is found sporadically with a number of bark beetles and thus its association with *P. pini* cannot be included among the specific associations (Mathiesen-Käärik 1960.)

According to Löyttyniemi and Uusvaara (1977), *Pissodes* larvae found in pine and spruce logs did not cause discoloration during six weeks of storage. If the logs were felled in southern Finland at the beginning of July or earlier, some logs became partly blue by the end of September, especially in the vicinity of the pupal chip cells. In the same study, most of the weevil individuals caught in window traps were *P. pini*; only a few specimens of *P. piniphilus* (Herbst) and *P. harcyniae* (Herbst) were trapped, but there is no direct evidence of specific fungal transmission.

3. VECTORS OF DECAY FUNGI

Larvae of the large pine weevil have been detected in the roots of Scots pine infected with the root-rot fungus *H. annosum* (Jørgensen and Beier Petersen 1951; Laine 1977). In the field, seedlings killed by root-rot are often wounded by the gnawing of pine weevils. Even small fruiting bodies are sometimes found around feeding scars made by the pine weevil (Laine 1977). *H. annosum* has been isolated from the excrement of large pine weevils collected in the field in Czech Republic (Kadlec *et al.* 1992). Furthermore, both the mycelium and the conidia of *H. annosum* have survived in viable condition through the digestive tract of the large pine weevil (Nuorteva and Laine 1972; Dušin 1979). However, on the basis of these experiments, it is unclear whether mycelium actually survived through the pine

Table 1. Root- and phloem-feeding weevils (Coleoptera: Curculionidae) and associated fungi.

Insect	*Fungus*	*References*
Hylobius sp.	*Leptographium procerum*	Jacobs *et al.* 2001
Hylobius abietis	*Heterobasidion annosum*	Nuorteva & Laine 1968; Laine 1977; Kadlec *et al.* 1992
	Leptographium alethinum	Jacobs *et al.* 2001
	Leptographium procerum	Piou 1993; Lévieux *et al.* 1994a
	Leptographium wingfieldii	Piou 1993
	Graphium canum	Piou 1993
	Ophiostoma piliferum	Piou 1993
Hylobius pales	*Leptographium procerum*	Lackner & Alexander 1982; Wingfield 1983; Lewis & Alexander, 1986; Alexander *et al.* 1988; Klepzig *et al.* 1991; Nevill & Alexander, 1992a,b,c
	Ophiostoma ips	Klepzig *et al.* 1991
	Ophiostoma piceae	Nevill & Alexander 1992a,c
	Graphium sp.	Klepzig *et al.* 1991; Nevill & Alexander 1992a
Hylobius radicis	*Ophiostoma ips*	Klepzig *et al.* 1991
	Leptographium procerum	Wingfield 1983; Alexander *et al.* 1988; Klepzig *et al.* 1991
	Leptographium terebrantis	Wingfield 1983; Klepzig *et al.* 1991
	Graphium sp.	Klepzig *et al.* 1991
Hylobius assimilis (=*H. rhizophagus*)	*Leptographium procerum*	Wingfield 1983; Alexander *et al.* 1988
	Leptographium terebrantis	Wingfield 1983
Pachylobius picivorus	*Leptographium procerum*	Wingfield 1983; Klepzig *et al.* 1991
Pissodes spp.	*Ophiostoma ips*	Klepzig *et al.* 1991
	Leptographium procerum	Livingston & Wingfield 1982; Lewis & Alexander 1986
	Armillaria mellea	Livingston & Wingfield 1982

Table 1. (continuation)

Insect	*Fungus*	*References*
Pissodes approximatus	*Leptographium procerum*	Lackner & Alexander 1982; Alexander *et al.* 1988
Pissodes castaneus	*Armillaria* spp.	Ehnström & Axelsson 2002
	Cronartium flaccidum	Alauzet 1972
	Ophiostoma spp.	Lévieux *et al.* 1994b
Pissodes fasciatus	*Leptographium wageneri*	Witcosky & Hansen 1985; Witcosky *et al.* 1986a; Witcosky 1989
Pissodes nemorensis	*Leptographium procerum*	Lackner & Alexander 1982; Nevill & Alexander 1992a b,c
	Ophiostoma piceae	Nevill & Alexander 1992a,c
	Graphium sp.	Nevill & Alexander 1992a
Pissodes piceae	*Ophiostoma canum*	Lévieux *et al.* 1994b
	Ophiostoma ips	Lévieux *et al.* 1994b
Pissodes pini	*Ophiostoma minus*	Mathiesen-Käärik 1953, 1960
	Heterobasidion annosum	Kangas 1938; Jørgensen & Beier Petersen 1951; Nuorteva & Laine, 1968; Laine 1977
	Leptographium procerum	Kendrick 1962; Livingston & Wingfield 1982
	Leptographium lundbergii	Mathiesen-Käärik 1953
	Aureobasidium pullulans	Mathiesen-Käärik 1960
Pissodes piniphilus	*Peridermium pini*	Kangas 1934; Pappinen & von Weissenberg 1994a,b
	Lachnellula pini (Brunch.) Dennis	Kangas 1938
	Ceratocystiopsis minuta	Mathiesen 1951
Steremnius carinatus	*Leptographium wageneri*	Witcosky & Hansen 1985; Witcosky *et al.* 1986a; Witcosky 1989

weevil digestive tract or whether the mycelium was originally contaminated with the conidia.

It has been suggested that a succession of fungi in roots wounded by *Hylobius* begins with the hyphomycetes or by other fungi usually not considered capable of causing extensive decay in wood and that later succession is followed by the decay fungi (Whitney 1961). Thus, in the Great Lakes region, *H. annosum* and *Armillaria* spp. have not been isolated from declining red pine, *Pinus resinosa* Ait. stands associated with the complex of scolytids, curculionids, *Leptographium* and *Ophiostoma* fungi (Klepzig *et al.* 1991; Erbilgin and Raffa 2002). Most decay fungi (except for *Armillaria* and some others) infect the stump from a cut surface. They grow relatively slowly down to the roots and in the early phases of colonization probably do not affect the suitability of the substrate for insect breeding. Nor are the larger roots, where the pine weevil breeds, reached rapidly by the soil fungi that penetrate the thin roots (von Sydow 1993). Consequently, it seems that the large pine weevil and most weevils breed without fungal interaction.

In Finland, larvae and pupae of *Pissodes pini* have been detected at the stem base of *H. annosum*- infected Scots pine (Nuorteva and Laine 1968). Fruiting bodies of *H. annosum* have also been found near the feeding wounds of *P. pini* (Nuorteva and Laine 1968; Laine 1977). In Denmark, Jørgensen and Beier Petersen (1951) have found *P. pini* gnawing trees infected by *H. annosum*. However, in all these cases it is unclear whether *P. pini* attacked trees weakened by root rot or whether the weevil fed first and root rot came later. Of the European *Pissodes* species, on some occasions *P. pini* has been speculated to be a primary pest on mature conifers.

4. VECTORS OF RESIN TOP DISEASE

The pine-top weevil, *P. piniphilus*, is considered to a important pest in Europe. However, the primacy of *P. piniphilus* has not yet been solved. *Tomicus piniperda* and *Tomicus minor* often attack trees where *P. piniphilus* has been breeding in a previous year (Ehnström and Axelsson 2002). The pine-top weevil and the small-banded pine weevil, *Pissodes castaneus* (De G.), often breed in pines that are weakened by resin-top disease caused by a rust pathogen *Peridermium pini* (Kangas 1934; Kudela 1974). On *Pinus pinaster* Ait. the association of *P. castaneus* with resin top disease caused 62% mortality, whereas mortality was lower in trees infected by the fungus alone (Alauzet 1972). However, also in all these cases it is unsure whether host trees were weakened by the fungus before weevil breeding or whether the fungus was disseminated after the weevil arrived.

Pappinen and von Weissenberg (1994a) found a positive correlation between *P. piniphilus* pupal chambers and disease frequency. The weevils were associated with stands that were heavily infected by the resin-top disease. The presence of canker favoured the breeding of *P. piniphilus*, while the number of pupal chambers was largest in the region of the canker. *P. piniphilus* has been found to carry spores in both field and laboratory conditions (Pappinen and von Weissenberg 1994b). Weevils were able to carry spores and infect healthy trees with spores while the time of weevil emergence and the development of new aecia were overlapping (Pappinen and von Weissenberg 1994a, b).

In a feeding test, *P. piniphilus* preferred diseased branches significantly more than healthy branches (Pappinen and von Weissenberg 1996). Furthermore, weevil feeding increased the germination of *P. pini* aeciospores on pine phloem and needle extracts. Especially in rust fungi, insect transfer leads to cross-fertilization, brings one mating type to another and results in high levels of local genetic diversity (Hunt 1985; Webber and Gibbs 1989; Hamelin 1996). Thus the migration and breeding habits of weevils may affect the incidence of disease on host trees.

5. ROOT DISEASES IN NORTH AMERICA

5.1. Black-stain root disease

Leptographium wageneri, which causes black-stain root disease, is characterized by dark staining in the roots and lower stem of mature conifers. *L. wageneri* colonizes a tree tangentially along the growth rings and thus only along the actively conducting xylem tracheids of the roots and stems, whereas radial growth is minor (Harrington and Cobb 1983). The disease fulfils the requirements of wilting disease by blocking water transport and finally leading to a decrease in the terminal growth of infected trees (Witcosky and Hansen 1985). Black-stain root disease is thought to be a native disease of Douglas-fir *Pseudotsuga menziesii* (Mirb.) Franco in western North America. There are three recognized host-specialized varieties, *L. wageneri* var. *wageneri* M.J. Wingf., which is pathogenic to pinions, the variety *ponderosum* T.C. Harr. & F.W. Cobb, which specializes on western hard pines, and the variety *pseudotsugae* T.C. Harr. & F.W. Cobb, which causes black-stain on Douglas-fir and hemlock species (Harrington and Cobb 1986; Zambino and Harrington 1989).

A root-feeding bark-beetle, *Hylastes nigrinus* (Mannerheim), and the root-feeding weevils *Steremnius carinatus* (Boheman) and *Pissodes fasciatus* LeConte are among the primary vectors (Harrington *et al.* 1985; Witcosky and Hansen 1985; Witcosky *et al.* 1986a; Hansen *et al.* 1988). In infected areas, apparently low numbers of vector insects, up to 5%, may be infested with *L. wageneri* during emergence and dispersal (Harrington *et al.* 1985; Witcosky *et al.* 1986a). *S. carinatus* causes, in particular, the tree-to-tree spread of the pathogen around established infections, while wounds caused by *P. fasciatus* are encountered less frequently on diseased trees (Hansen *et al.* 1988). Adults of *S. carinatus* are flightless, and *P. fasciatus* feeds only on dead and dying trees, which restricts their ability to spread root pathogens. However, both weevils carry *L. wageneri* in the field, transmit the fungus to host trees, and feed or oviposit on susceptible hosts under conditions suitable for transmission of *L. wageneri*, thus fulfilling the postulates of the vector hypothesis (Leach 1940; Witcosky and Hansen 1985; Witcosky *et al.* 1986a).

Black-stain root disease is most often found in 5- to 30-year-old plantations that have been pre-commercially thinned (Harrington *et al.* 1983, 1985; Hansen *et al.* 1988; Witcosky *et al.* 1986a, b). Clear cutting and thinning activities increase weevil populations at such sites (Harrington *et al.* 1985; Witcosky *et al.* 1986a, b). Even in the absence of vector activity, the fungus can cause mortality of seedlings and large trees through root graft transmission (Hessburg and Hansen 1986; Harrington 1988). In areas with high risk of black-stain root disease, thinning should be avoided or done immediately after the flight period so that the host material can age and lose much of its attractiveness (Witcosky *et al.* 1986b; Witcosky 1989). Forest management has created favourable conditions for root-feeding insects and for the fungus causing black-stain root disease.

Damage due to the black-stain root disease in thinned stands has been suggested to be a result of the behavioural preferences of its insect vectors. Large areas of young susceptible stands have increased the occurrence of root disease. The fungus *L. wageneri* does not have cellolytic enzymes for penetration of cell walls. Different host-specialized varieties of black-stain fungi attack Douglas-fir and lodgepole pine *Pinus contorta* Dougl. ex Loud. All these features together indicate that the fungus is able to adapt to different habitats; and they make black-stain root disease extremely harmful, if it manages to spread into managed forests in Europe.

5.2. Leptographium terebrantis

Leptographium terebrantis Barras and Perry is, together with *L. procerum*, among the causal agents of red pine decline on *P. resinosa* in the United States. *L. terebrantis* causes the black-staining of primary roots, lesions in the phloem and resin-soaking areas in the lower stem and root-collar (Harrington and Cobb 1983; Raffa and Smalley 1988). The typical symptoms in a forest are openings formed by dead and diseased trees in various stages of decline. This fungus is weakly pathogenic and colonizes, in particular, stressed or wounded conifers. *L. terebrantis* and *L. wageneri* are more virulent than *L. procerum* (Harrington and Cobb 1983; Wingfield 1983, 1986).

The fungus is associated with various bark beetles, *D. terebrans* Oliver, *D. valens* LeConte and *Hylurgops porosus* (LeConte) (Harrington and Cobb 1983; Owen *et al.* 1987); but it has also been isolated from trees infested by the root-collar weevil *H. radicis* Buchanan (Wingfield 1983; Klepzig *et al.* 1991). However, in the absence of *L. procerum* Wingfield (1983) could not isolate *L. terebrantis* from any of the trees infested by the root-collar weevil. Thus, the role of the fungus in this disease is speculative – neither of the abovementioned fungal agents have been shown to cause the disease independently.

5.3. Procerum root disease

Leptographium procerum is common on pines and is speculated to cause white pine root decline on *P. strobus*. The symptoms are presence of resinous streaks from roots to stem base, sapwood discoloration, decreased shoot growth and needle wilting. The weevils and bark beetles transmit the fungus from infected trees to the roots of healthy but stressed trees. *L. procerum* is considered to be a weak wound pathogen that is unable to kill seedlings when wound-inoculated into a stem

(Harrington and Cobb 1983; Wingfield 1983). The pathogenicity of this species has been a matter of substantial debate (Jacobs and Wingfield 2001). The discrepancy may be caused by different inoculation methods, variation in the pathogenicity of fungal strains or simply that the fungus is not a primary pathogen.

Leptographium procerum is associated with several root and root-collar infesting insects in the eastern parts of North America. Mainly the pine-reproducing weevils, *Hylobius pales* Herbst, *H. radicis*, *H. assimilis* (Bohemann) (*H. rhizophagus* M., B. & W.), *Pachylobius picivorus* (Germar) and *Pissodes nemorensis* Germar, carry *L. procerum* (Wingfield 1983; Lewis and Alexander 1986; Alexander *et al.* 1988; Raffa and Smalley 1988; Nevill and Alexander 1992b, c). Furthermore, *L. procerum* is found in the galleries of *Pissodes approximatus* Hopkins (Herbst) on pine (Wingfield 1983; Alexander *et al.* 1988). Under controlled conditions, weevils seem to transmit *L. procerum* to fresh white pine bolts more effectively than bark beetles do (Lewis and Alexander 1986). In addition, *L. procerum* is commonly isolated from surface-sterilized *H. radicis*, *H. pales* and *P. picivorus*, and less frequently from *D. valens* (Wingfield 1983).

As the pathogen spreads throughout the root collar, the infected tissue becomes more suitable for weevil oviposition and breeding. *H. pales* and *P. nemorensis* normally oviposit in stressed or diseased trees, not on healthy ones, as *H. radicis* does. *H. radicis* causes symptoms on pines similar to those associated with white pine root decline, although it seldom infests five-needle pines (Wingfield 1983, 1986). Wingfield (1983) isolated *L. procerum* from roots that had been recently damaged by weevils, but not from roots damaged during previous years and already decaying. Furthermore, the low recovery of the fungus from the soil suggests dissemination by the insect (Lewis *et al.* 1987). Leach's postulates about the vectorship are fulfilled when weevils transmit *L. procerum*. At first, weevils are associated with diseased trees (Leach 1940; Lackner and Alexander 1982; Wingfield 1983, Nevill and Alexander 1992b). Secondly, weevils are found with their host trees during their whole life cycle (Raffa and Klepzig 1996). Furthermore, *H. pales* and *P. nemorensis* weevils carry *L. procerum* in the field (Wingfield 1983) and finally, weevils are able to transmit the fungus to a healthy plant (Lackner and Alexander 1982; Lewis and Alexander 1986; Nevill and Alexander 1992c). It is important to note that Leach's postulates relate to the vectorship – but Koch's postulates are a prerequisite to show primary pathogenicity – for *L. procerum* and *L. terebrantis* (in the field) this has never been achieved.

6. CONCLUSIONS

The ecological role of root-feeding weevils and the fungi with which they are associated is obscure. If weevils are associated with fast-growing pathogenic fungi, they compete for the same nutrient resources. This points out what Berryman (1989) has suggested that co-adaptation of the weevils with fungal pathogens is not an evolutionarily stable strategy.

In *L. wageneri*, the sexual state of *Ophiostoma wageneri* (Goheen and F.W. Cobb) T.C. Harr. has been found only in the galleries of *Hylastes*; thus it is possible that the fungus needs root-inhabiting insects to bring the compatibility types together (Goheen and Cobb 1978). Whether lack of a functional sexual state is an indication that the weevils play some role in dissemination of root-infecting pathogens, is a highly speculative idea.

On white pine it has been demonstrated that adult weevils locate and oviposit on trees with roots diseased by *L. procerum* in advance of bark beetles (Nevill and Alexander 1992b). Whether European root-feeding weevils play a special role in inhabiting weakened seedlings and trees before the bark beetles remains to be solved.

The phrase "out of sight, out of mind" describes well the role of subterranean and sub-cortical insects in many ecosystems (Hunter 2001). In many cases, delimitation of species for instance within *Leptographium* is difficult and requires studies on the ultra-structure of fungal spores. Difficulties in identification may have inhibited detection of associated fungi. Both in the assessment of root-feeding insect abundance and their possible fungal associates, there is a clear gap in our knowledge.

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