

Exotic invasive elm bark beetle, *Scolytus kirschii*, detected in South Africa

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IN FEBRUARY 2005, THE EXOTIC BARK BEETLE, *Scolytus kirschii* (Curculionidae: Scolytinae), was detected infesting English elms (*Ulmus procera*) in Stellenbosch, South Africa. This appears to be the first report of an infestation of *Scolytus* species in this country. The presence of this beetle is of concern for several reasons. *Scolytus kirschii* is a serious pest of elms, capable of killing healthy trees, resulting in considerable economic impact. There also exists the possibility that the beetle may undergo a host switch to indigenous trees, with potentially serious ecological consequences. Furthermore, the beetle is capable of being the vector of the pathogens responsible for Dutch elm disease (DED), *Ophiostoma ulmi* and *Ophiostoma novo-ulmi*. None of the trees that we inspected in Stellenbosch exhibited symptoms or signs of DED. Isolations from infested host material likewise failed to detect these pathogens. Nonetheless, the damage to the trees by the beetles alone was sufficient to cause tree death. Future directions for research and management of the beetle in its new environment are discussed.

Introduction

In February 2005, the exotic bark beetle, *Scolytus kirschii* Skalitzky[#] (Curculionidae, Scolytinae), was detected infesting several large English elms (*Ulmus procera*) growing on a farm in Stellenbosch, South Africa. Within two weeks of the initial discovery, infested English elms were also detected at a second site in Stellenbosch.

To the best of our knowledge, this is the first report of an infestation of *Scolytus* species in South Africa. It also appears to be the first account of the establishment of *S. kirschii* outside southern and central Europe, the Mediterranean, and Central Asia.^{3,5,8-11} At this time, it is not known whether the distribution of *S. kirschii* in South Africa is restricted to Stellenbosch

[#]The original spelling of the specific name *kirschii* by Skalitzky¹ is valid and is retained here (ICZN 1999, article 31).² although some later authors have used the spelling *kirschi*.³⁻⁷

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or whether it is more widespread. It is also not known how long the beetle has been present in South Africa, how it gained entry, or whence it originated. However, the beetle's presence in South Africa is of considerable concern owing to its ability to kill ornamental elms, the potential that it may switch hosts from exotic elms to related indigenous trees, and its potential impact as a vector of the causal agents of Dutch elm disease (DED), *Ophiostoma ulmi* and *O. novo-ulmi*.

In this paper, we present a brief introduction to the biology of *S. kirschii* in its range outside South Africa. We also summarize our initial observations of the beetle in elms in Stellenbosch, and discuss the potential adverse effects the insect may have on biodiversity and on ecologically and commercially important tree species in South Africa. Future directions for research and management of the beetle in its new environment are also suggested.

Biology and morphology of *Scolytus kirschii*

Very little is known of the biology of *S. kirschii* in its native range. The information we present here was compiled from records from parts of central and southern Europe, Tajikistan, Russia, and Israel.^{3,5,6,9,10,12} It is unclear whether the beetle is indigenous or was introduced to Israel; however, it appears likely that it is exotic to that region.¹⁰

Adult beetles are very small (1.5–3.0 mm in length), elongate, and reddish-brown (Fig. 1), with elytra that cover the posterior portion of the abdomen. The sternites ascend steeply to meet the elytra and possess long, semi-erect hairs (Fig. 2). A central spine is present on the anterior margin of the second abdominal sternite (Fig. 3).

Scolytus kirschii is monogamous. Females attack the trees and initiate galleries in the phloem layer just beneath the outer bark, where breeding occurs. Egg galleries are constructed following the grain of the wood and larval galleries extend at right angles away from the egg galleries, typically, but not always, directed against

the grain (Fig. 4). In central Europe and Russia, egg gallery length ranged 5–25 mm and brood production was estimated at 4–14 per pair.³⁻⁵ It has been suggested that each female is responsible for multiple galleries.³ However, in Israel, egg gallery length was observed to range 15–65 mm and the number of eggs produced per parental pair was estimated at 50–130.¹⁰ A single generation per year was reported from Russia and central Europe,^{3,5} whereas in Israel the beetle produces four to five generations annually and overwinters as mature larvae.¹⁰

Preferences for breeding substrate appear to vary somewhat among populations. The different hosts utilized in each region may account for some of this variation. In Israel, primarily stems and branches 2–11 cm in diameter were used for breeding,¹⁰ while in Spain and Portugal breeding was mostly confined to twigs and branches 1–5 cm in diameter, although occasionally larger material was also used.¹² Maturation feeding (feeding by adult beetles in phloem tissues independent of production of brood) is reported to occur primarily in forks of small branches and twigs and at the base of leaf petioles.^{5,6}

Scolytus kirschii appears restricted to colonizing trees in the genus *Ulmus*, although within *Ulmus* it can be considered a generalist, attacking all species that it encounters.^{5,6,10} Records from other hosts such as *Prunus* species, *Fraxinus excelsior* and *Populus alba*,^{5,9} probably refer to accidental, non-breeding attacks.⁴ While many *Scolytus* prefer or are restricted to colonizing weakened trees, some species are highly aggressive and capable of successfully attacking and killing healthy trees.⁶ In Israel, Spain and Portugal, *S. kirschii* is reported to attack drought-stressed, but otherwise healthy elms,^{10,12} while in Russia and Tajikistan, the beetle is considered highly aggressive and able to kill healthy, vigorous young and mature trees.^{3,5,6}

The beetle is one of several scolytine species that are known or suspected to be the vector of the causal agents of DED, *Ophiostoma ulmi* and *O. novo-ulmi*.¹²⁻¹⁷ The effectiveness of *Scolytus* species as vectors in transmission of the disease is directly related to the spore load that the beetles carry. *Scolytus kirschii* in its native range is not considered to be an efficient vector in the transmission of DED. It is a relatively tiny beetle and carries correspondingly small spore loads in contrast to other, larger *Scolytus* species.¹² Webber found that the spore loads carried by this beetle fall well below that required to be successful in infecting *U. procera*, a moderately

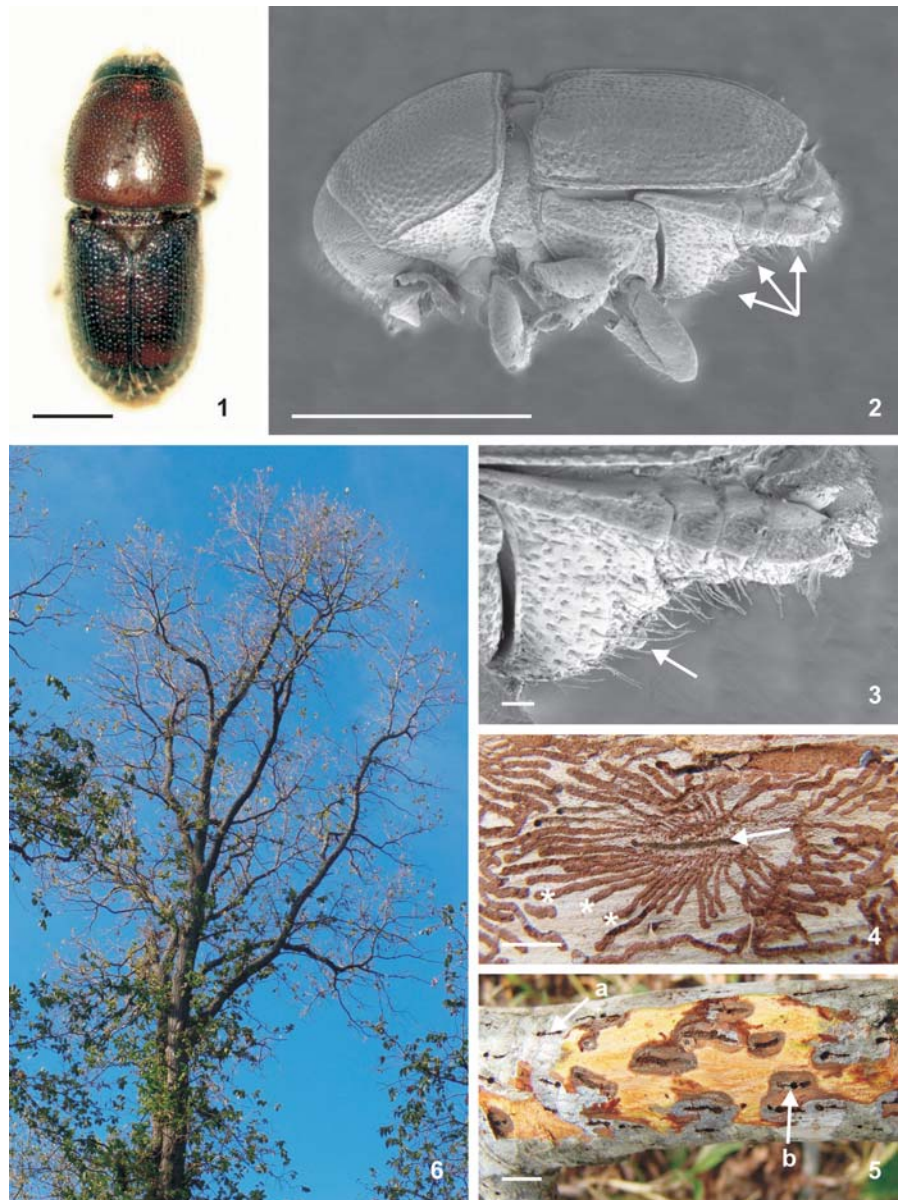
susceptible host.¹² Furthermore, in its natural range, *S. kirschii* tends to breed in branches and twigs of small diameter that are prone to relatively rapid desiccation. In these small-diameter branches the bark above the breeding galleries often splits, further accelerating the rate of drying.¹² Under dry conditions, the DED pathogens are unlikely to sporulate in beetle pupal chambers and, consequently, newly emerging adult beetles developing in such material are unlikely to acquire spores prior to dispersal, and thus are unlikely to vector the pathogens.¹²

In a recent study on phoretic mites associated with two other elm bark beetles, *S. multistriatus* and *S. pygmaeus*, the possibility is mentioned that certain mites might play a role as vectors of *O. novo-ulmi*.¹⁸ Although nothing about the mites associated with *S. kirschii* has been published, the presence or absence of mites with the beetles in South Africa needs to be established.

Scolytus kirschii in South Africa

The infested trees observed at the first site in Stellenbosch where the beetles were detected were large, mature *U. procera* (English elm) that were healthy and well-watered at the time of attack. Of eight infested trees, one had died and had been cut for firewood. The remaining trees were alive but had sustained such extensive damage (Fig. 6) that they are likely to die within the coming year. Damage due to maturation feeding by the beetles in twig and branch forks was commonly observed; however, it was the densely spaced, short (average length 10 mm), non-breeding galleries present on most, if not all, medium and small diameter branches that were responsible for most of the damage to the trees. These non-breeding galleries were easy to locate owing to their sheer abundance and the vertical cracks in the outer bark that developed over each gallery (Fig. 5). We consider these galleries to be the result of maturation feeding, as no eggs, egg niches, or brood were ever found associated with them. At the second site where beetles were detected, the effects and colonization patterns of the beetles in infested trees were similar to those observed in trees at the first site.

Breeding galleries were primarily observed in the large branches (approximately 25–40 cm in diameter) of the tree that had been killed. In these branches, beetles had already completed development and emerged; however, bark remained intact (no cracks) over galleries. Few breeding galleries were observed



Figs 1–6. The infestation of English elm trees near Stellenbosch by the exotic bark beetle, *Scolytus kirschii*. 1, Adult beetle (light microscope, bar = 0.5 mm). 2, Scanning electron micrograph of the adult female beetle, showing steeply ascending sternites (arrows) with abundant hairs (bar = 1.0 mm). 3, Prominent spine on the second sternite (bar = 0.1 mm). 4, Breeding galleries consist of several larval galleries (*) extending at right angles away from a central, longitudinal egg gallery (arrow) (bar = 10 mm). 5, Maturation feeding of the beetles causes vertical cracks in the bark covering galleries (a) and a discoloration of the sapwood underneath the bark, surrounding galleries (b) (bar = 10 mm). 6, Large *Ulmus procera* tree dying as a result of beetle infestation.

in the still-living trees; those that were observed occurred in small diameter (approximately 1 cm) twigs. No cracks were associated with these galleries; however, the twigs were still relatively green. Egg galleries in the larger diameter branches ranged from 7–27 mm in length (mean = 15.6, s.e. = 1.8, $n = 12$) and the number of eggs per gallery (estimated by counting egg niches and larval galleries) ranged from 15–43 (mean = 28.4, s.e. = 2.4, $n = 12$). In the smaller diameter twigs of the living trees, the length of the egg galleries ranged from 7–11 mm (mean = 8.6, s.e. = 1.2, $n = 3$) and the number of eggs from 9–14 (mean = 11.7, s.e. = 2.5,

$n = 3$). Our estimates of egg production from galleries in twigs agree with estimates for beetles in France that breed in small-diameter substrates.⁴ However, our estimates of egg production in large-diameter branches were greater than those for beetles in Russia,³ but substantially below those for beetles colonizing branches of moderate diameter in Israel.¹⁰

Because some *Scolytus* species act as vectors of the causal agents of DED, we also assessed the infested trees for symptoms and signs of infection by *O. ulmi* or *O. novo-ulmi*. Although the living trees were clearly in decline due to mass attack and physical damage by the beetles, none

of the trees exhibited symptoms of DED such as wilt or brown streaking of cambial and xylem regions, nor signs of the pathogens including perithecia, synnemata or conidiophores in beetle-breeding or non-breeding galleries, or pupal chambers. Microscopic inspection of maturation feeding grooves in branch forks, breeding and non-breeding galleries, and pupal chambers revealed only common saprophytic fungi as did cross sections of branches incubated for up to two weeks in humid chambers. Isolations from galleries, feeding grooves, pupae, and adult beetles on selective media (malt extract agar amended with cycloheximide and streptomycin)¹⁹ likewise failed to detect the pathogens.

Potential impacts of *Scolytus kirschii* in South Africa

The presence of non-indigenous species can have serious ecological and economic consequences in the area of introduction.²⁰ Impacts on trees affected by exotic species can include direct economic effects including reduced growth, increased mortality, as well as a fall in property values, and the costs of control measures and implementation of regulations.²⁰ Less easily measured, but equally important, are the often devastating ecological consequences for indigenous ecosystems. These may include the reduction in range or numerical abundance, or even local extinction, of indigenous species, alterations in ecosystem structure and interspecies dynamics, and changes in biological diversity.²⁰

The introduction of *S. kirschii* into South Africa has several potential economic and ecological implications. A major concern is its possible influence on ornamental plantings of the fourteen *Ulmus* species and hybrids (all exotic) that occur in South Africa.²¹ As a generalist on *Ulmus*, *S. kirschii* could attack and breed in any of these elms. However, it is likely that this beetle, like other elm-feeding *Scolytus* species, will exhibit distinct feeding preferences, preferring some species while feeding at lower levels on others.^{16,17,22-24} Consequently, only some elm species in South Africa are likely to be at high risk of damage or mortality by the beetle. Our observations in Stellenbosch indicate that *U. procera* is one of these. What other species are likely to be preferred by the beetle and at risk remains unknown.

Elms are often prized for their beauty and shade, which has resulted in their extensive use as ornamentals in gardens and street plantings and in practical use as windbreaks and to provide shade to live-

stock.²⁵ The death of mature trees can result not only in a loss of these functions but also in considerable economic costs associated with tree removal and replacement and reduced property values. The loss of large trees is not easily remedied because of the long time required for replacement trees to grow. Furthermore, dead trees left in place are unsightly and pose risks to human safety. Efforts to protect living trees from beetles are also likely to prove costly, both economically and ecologically. Such efforts would include increased pesticide use and its associated economic and ecological impacts, and increased irrigation to reduce susceptibility of trees to beetle attack, placing higher demands on limited water resources.

Potential risks to non-*Ulmus* species also need to be considered. While *S. kirschii* is known to attack *Ulmus* species mainly in their native range, a number of other elm-feeding *Scolytus* species also infest hosts in other genera within the Ulmaceae. For example, both *Ulmus* and *Zelkova* are hosts for *S. ensifer*, *S. eichhoffi*, *S. multistriatus*, *S. scolytus*²⁶ and *S. japonicus*.¹¹ Other genera of Ulmaceae attacked by *Scolytus* species include *Planera* and *Celtis*.⁸ Shifts onto novel hosts, especially those in closely related genera, by exotic organisms in new environments, are not unknown²⁷⁻²⁹ and can result in devastating effects on native ecosystems.³⁰

Trees in several genera of the Ulmaceae occur in South Africa. These include seven species of *Celtis* (three native, four exotic), one species of *Zelkova* (exotic), one species of *Trema* (native), and one of *Chaetacme* (native).^{21,31} Potential effects on indigenous tree species are of special concern. Exotic organisms can cause the decline or even extinction of native plants and trees, which in turn cause cascading indirect effects that can alter entire biological communities.^{32,33} While the likelihood is small that *S. kirschii* will switch hosts to indigenous trees, related indigenous trees in the Ulmaceae should be monitored.

The European elm bark beetle, *Scolytus multistriatus*, has been accidentally introduced into both New Zealand³⁴ and Australia, where it causes substantial damage.^{35,36} It is intriguing that the insect is present in Australia in the absence of the DED pathogen *Ophiostoma novo-ulmi*,³⁷ but that both insect and pathogen are present in Auckland.³⁴ After the discovery of DED in New Zealand 1989, an intensive eradication programme was conducted.³⁴ Despite very substantial investments, small numbers of infected trees continue

to be found.³⁸ Nevertheless, the eradication programme is continuing in order to prevent the spread of the disease to elms or potentially to native trees in other parts of New Zealand.³⁸ In the absence of the DED pathogen, *S. multistriatus* does not cause serious damage to ornamental elms in Victoria, but this invasion would have been substantially more serious if the DED pathogen were present.³⁷ An anamorphic basidiomycete, *Michenera artocreas*, has been linked to *S. multistriatus* in Australia, but its pathogenicity and the fungus-beetle association is unclear.³⁵ The invasion of *S. kirschii* in South Africa is similar to that in Australia in the sense that the insect is present without the DED pathogen. However, the impact that *S. kirschii* is having on elms in Stellenbosch appears to be substantially more severe than that reported for *S. multistriatus* in Australia.³⁷

While *S. kirschii* is not considered a highly effective carrier of the DED pathogens in other regions of the world,¹² it should not be completely dismissed as a potential vector in the transmission of the disease in South Africa should *O. ulmi* or *O. novo-ulmi* be introduced. Many factors including spore load, phoretic mites, environmental conditions, feeding preference, and host tree susceptibility interact to determine whether a beetle will be an efficient vector in a particular location.^{17,18} While spore loads carried by the beetle are typically small and insufficient to cause infection in resistant or moderately susceptible hosts,¹² they may be sufficient to cause infection in highly susceptible hosts.¹⁵ Furthermore, in South Africa we observed the beetle breeding in branches of very large diameter with uncracked bark. Unlike the smaller diameter substrate used by the beetle in other regions, such large material may retain sufficient moisture to support sporulation of the pathogens, resulting in a higher spore load of dispersing beetles.

Future efforts

Pathways of entry for wood-utilizing insects are most often casewood, palettes, or dunnage.²⁹ With *S. kirschii*, the pathway of entry into South Africa most likely included one of these materials constructed of elm wood with bark attached. The possibility of other *Scolytus* species, such as *S. multistriatus*, with the DED pathogens entering through the same route, is alarming. The implementation and strict enforcement of regulations against the ingress of such material, especially that with attached bark, would greatly reduce the potential for reintro-

duction of these and other wood-associated insects.

One of the first steps in response to the presence of *S. kirschii* should be to determine the distribution of the beetle in South Africa. If the spread is limited and infestations are localized, procedures aimed at eradicating the beetle, including the removal and destruction of infested trees should be implemented as soon as is feasible. At the same time, efforts should be made to determine the location and mode of entry of the beetle, so that if eradication is successful, measures can be taken to avoid future reintroductions. In addition, an effort should be made to determine whether *S. kirschii* is able to infest native Ulmaceae and especially species of *Celtis* such as *C. africana*. These trees could be threatened by the invasion of the insect and an early warning of this possibility would be useful.

The detection of *S. kirschii* should serve as a reminder that exotics pose significant risks to the resources of South Africa. Considerable effort must be made to identify, monitor and regulate pathways of these organisms to avoid their introduction and associated consequences. Avoidance is the best approach. If organisms gain entry, however, early detection can greatly reduce economic damage to commercially valuable resources and sometimes allow for successful eradication. While new introductions of exotics are often quickly detected in commercial forests and in ornamental plantings, allowing rapid action against the organisms, this is not always the case with indigenous forests, where changes are often subtle and not easily noticed. Therefore, a system should be implemented to monitor indigenous forests and woody ecosystems at risk of invasion by exotics. Concurrently, there is a need for research to survey the native insect pests and diseases associated with indigenous woody plants, which are poorly known and largely undescribed. In the absence of such baseline knowledge,²⁹ new introductions are likely to pass unnoticed for extended periods of time.

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- Skalitzky K. (1876). *Scolytus kirschii* Skal. *Entomol. Monatsbl.* **1**, 110.
- International Commission on Zoological Nomenclature (1999). *International Code of Zoological Nomenclature*, 4th edn. International Trust for Zoological Nomenclature, London.
- Escherich K. (1923). *Die Forstinsekten Mitteleuropas, Band 2 (Urinsekten, Geradflügler, Netzflügler und Käfer)*. Paul Parey Verlag, Hamburg & Berlin.
- Balachowsky A. (1949). *Faune de France*, vol. 50. *Coleopteres, Scolytides*. Lechevalier, Paris.
- Postner M. (1974). Scolytidae (Ipidae), Borkenkäfer. In *Die Forstschädlinge Europas, Band 2 (Käfer)*, ed. W. Schwencke, pp. 334–482. Paul Parey Verlag, Hamburg & Berlin.
- Kadyrov A.Kh. (1989). On the bark beetles (Coleoptera: Scolytidae) of Southwestern Tajikistan. *Entomol. Rev.* **68**, 12–18.
- Wood S.L. and Bright D.E. (1992). A catalog of Scolytidae and Platypodidae (Coleoptera), Part 2: Taxonomic index. *Great Basin Nat. Mem.* **13**, 1–1553.
- Michalski J. (1973). *Revision of the Palearctic species of the genus Scolytus Geoffroy (Coleoptera: Scolytidae)*. Polska Akademia Nauk, Warsaw.
- Freude H., Harde K.W. and Lohse G.A. (1981). *Die Käfer Mitteleuropas, Band 10 (Bruchidae, Anthribidae, Scolytidae, Platypodidae, Curculionidae)*. Goecke & Evers Verlag, Krefeld.
- Halperin J. (1986). The elm beetle *Scolytus kirschii* and its control in Israel. *EPPA Bull.* **16**, 593–595.
- Yanovskii V.M. (1999). Annotated list of scolytids (Coleoptera, Scolytidae) of North Asia. *Entomol. Rev.* **79**, 493–522.
- Webber J.F. (1990). Relative effectiveness of *Scolytus scolytus*, *S. multistriatus* and *S. kirschii* as vectors of Dutch elm disease. *Eur. J. Forest Pathol.* **20**, 184–192.
- Brasier C.M. (1991). *Ophiotoma novo-ulmi* sp. nov., causative agent of current Dutch elm disease pandemics. *Mycopathologia* **115**, 151–161.
- Basset Y., Favaro A., Springate N.D. and Battisti A. (1992). Observations on the relative effectiveness of *Scolytus multistriatus* Marsham and *Scolytus pygmaeus* Fabricius (Coleoptera: Scolytidae) as vectors of the Dutch elm disease. *Mitt. Schweiz. Entomol. Ges.* **65**, 61–67.
- Faccoli M. and Battisti A. (1997). Observations on the transmission of *Ophiotoma ulmi* by the smaller elm bark beetles (*Scolytus* spp.). In *Integrating cultural tactics into the management of bark beetles and reforestation pests*, eds J.C. Gregoire, A.M. Liebhold, E.M. Stephen, K.R. Day and S.M. Salom, pp. 172–176. USDA Forest Service General Technical Report NE-236.
- Webber J.F. (2000). Insect vector behavior and the evolution of Dutch elm disease. In *The Elms: Breeding, Conservation, and Disease Management*, ed. C.P. Dunn, pp. 47–60. Kluwer Academic Publishers, Boston.
- Webber J.F. (2004). Experimental studies on factors influencing the transmission of Dutch elm disease. *Invest. Agrar.: Sist. Recur. For.* **13**, 197–205.
- Moser J.C., Konrad H., Kirisits T. and Carta L.K. (2005). Phoretic mites and nematode associates of *Scolytus multistriatus* and *Scolytus pygmaeus* (Coleoptera: Scolytidae) in Austria. *Agric. Forest. Ent.* **7**, 169–177.
- Harrington T.C. (1981). Cycloheximide sensitivity as a taxonomic character in *Ceratocystis*. *Mycologia* **73**, 1123–1129.
- Allen E.A. and Humble L.M. (2002). Nonindigenous species introductions: a threat to Canada's forests and forest economy. *Can. J. Plant Pathol.* **24**, 103–110.
- Glen H.F. (2002). *Cultivated Plants of South Africa*. Jacana Publishers, Johannesburg.
- Webber J.F. and Kirby S.G. (1983). Host feeding preferences by *Scolytus scolytus*. In *Research on Dutch elm disease in Europe*. *Forest. Commission Bull.* **60**, 47–49.
- Sacchetti P., Tiber R. and Mittempergher L. (1990). [Preference of *Scolytus multistriatus* Marsham in twig-crotch feeding on two elm species]. *Redia* **73**, 347–354. [Italian, English summary].
- Collin E., Rusanen M., Ackzell L., Bohnens J., Aguiar D.-A., Diamandis S., Franke A., Gil L., Harvengt L., Hollingsworth P.M., et al. (2004). Methods and progress in the conservation of elm genetic resources in Europe. *Invest. Agrar.: Sist. Recur. For.* **13**, 261–272.
- Poynton R.J. (1984). *Characteristics and Uses of Selected Trees and Shrubs Cultivated in South Africa*. Directorate of Forestry, Department of Water Affairs and Forestry, Pretoria.
- Pfeffer A. (1995). *Zentral- und Westpaläarktische Borken- und Kernkäfer*. Pro Entomologia, Basel.
- Smith D.M. (1976). Changes in eastern forests since 1600 and possible effects. In *Perspectives on Forest Entomology*, eds J.E. Anderson and H.K. Khaya, pp. 3–20. Academic Press, New York.
- Brockhoff E.G. and Bain J. (2000). Biosecurity implications of exotic beetles attacking trees and shrubs in New Zealand. *New Zeal. Plant Prot.* **53**, 321–327.
- Ridley G.S., Bain J., Bulman L.S., Dick M.A. and Kay M.K. (2000). *Threats to New Zealand's Indigenous Forests from Exotic Pathogens and Pests*. Science for Conservation No. 142. Department of Conservation, Wellington.
- Liebhold A.M., MacDonald W.L., Bergdahl D. and Mastro V.C. (1995). Invasion by exotic forest pests: a threat to forest ecosystems. *Forest Sci. Monogr.* **30**, 1–49.
- Coates Palgrave K. (1977). *Trees of Southern Africa*, 1st edn. Struik, Cape Town.
- McEvoy P.B. (2002). Insect-plant interactions on a planet of weeds. *Entomol. Exp. Appl.* **104**, 165–179.
- Crooks J.A. (2002). Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. *Oikos* **97**, 153–166.
- Gadgil P.D., Bulman L.S., Dick M.A. and Bain J. (2000). Dutch elm disease in New Zealand. In *The Elms: Breeding, Conservation and Disease Management*, ed. C.P. Dunn, pp. 189–199. Kluwer Academic Publishers, Boston.
- Parbery D.G. and Rumba K.A. (1991). *Michenera artocreas* in elm wood infested with *Scolytus multistriatus* in Australia. *Mycol. Res.* **95**, 761–762.
- Rosel A. and French J. (1974). Dutch elm disease beetle in Australia. *CSIRO Forest Prod. Newslett.* **398**, 6–8.
- Neumann F.G. and Minko G. (1985). Studies on the introduced smaller European elm bark beetle, *Scolytus multistriatus*, a potential vector of Dutch elm disease in Victoria. *Aust. Forest.* **48**, 116–126.
- Bulman L. and Dick M. (2004). Dutch elm disease 2003/04. *Forest Health News* **138**, 1.