Biology and Management of Root-Feeding Beetles (Coleoptera: Curculionidae) in North American Conifer Forests and Plantations

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Abstract

Root-feeding beetles, including several species of Hylastes Erichson (Coleoptera: Curculionidae), Hylurgops LeConte (Coleoptera: Curculionidae), Hylobius Gemar (Coleoptera: Curculionidae), Pachylobius LeConte (Coleoptera: Curculionidae), Pissodes Gemar (Coleoptera: Curculionidae), and Steremnius Schönherr (Coleoptera: Curculionidae), have emerged as serious problems in conifer plantations and forests in the United States and Canada in recent decades. Root-feeding beetles are particularly associated with stressed, diseased, or injured trees. Emerging adults kill seedlings by girdling them at the root collar and kill older trees, at least in the North and West, by transmitting fungal root pathogens in the genus Leptographium Lagerberg & Melin (Ophiostomatales: Ophiostomataceae). In the South, seedling mortality can be as high as 60% for seedlings planted in winter following fall harvest. For stands harvested after 1 July, planting should be delayed a full year. Broadcast insecticides can be used, but dipping seedlings in 0.75% permethrin prior to planting and physical barriers to feeding have proven effective. However, an integrated pest management approach that emphasizes a combination of measures to minimize attraction of beetles and to maintain health of host trees is recommended. Shelterwood harvest and soil scarification can create site conditions that minimize attraction of root beetles. Precommercial thinning and prescribed fire are often used to reduce tree competition and reduce vulnerability to stem-colonizing bark beetles. However, root beetles are attracted to thinned or burned stands, for at least 6–7 mo. Therefore, thinning should be avoided in areas of high risk for root disease transmission or, when necessary, thinning should be implemented during June or July following beetle dispersal in May. Semiochemicals can be used to monitor abundances of root beetles.

Key words: thinning, prescribed fire, semiochemicals, root disease
with effectiveness for both groups. Ing bark beetles, integrated management systems must be consistent available. Because these beetles co-occur with various stem-coloniz- tive measures will be emphasized, although some remedial tools are prevention during most of their life cycles. Therefore, preventa- beetles and associated pathogens are largely inaccessible for con- but their general interactions and management are similar. These onize conifers in different regions of the United States and Canada, species that feed on conifer roots. Different beetle assemblages col-

et al. 2013). This paper describes biology and management options for major species that feed on conifer roots. Different beetle assemblages colonize conifers in different regions of the United States and Canada, but their general interactions and management are similar. These beetles and associated pathogens are largely inaccessible for control measures during most of their life cycles. Therefore, preventative measures will be emphasized, although some remedial tools are available. Because these beetles co-occur with various stem-colonizing bark beetles, integrated management systems must be consistent with effectiveness for both groups.

Species Descriptions

Several species of Hylastes and Hylurgops (Coleoptera: Curculionidae: Scolytinae) are particularly important in Douglas-fir and pine plantations and forests across the western, north central, and southeastern United States. Bark beetles in this genus are relatively small (4–6 mm long), reddish-brown-to-black and cylindrical, resembling related bark beetles (Fig. 1; Drooz 1985; Furniss and Carolin 1992).

Hylastes mager LeConte (Coleoptera: Curculionidae) and Hylastes nigrinus (Mannerheim) (Coleoptera: Curculionidae) are the two most important vectors of black-stain root disease, Leptographium wageneri (Kendrick) (Ophiostomatales: Ophiostomataceae), in Douglas-fir and ponderosa pine plantations in the western United States. Adult H. mager are 5–6 mm in length and colonize roots of ponderosa and other pines, as well as Engelmann spruce, Picea engelmannii Parry ex Engelm. (Pinales: Pinaceae), from British Columbia to California and east to South Dakota and New Mexico. Adult H. nigrinus are about 4 mm in length and colonize roots of Douglas-fir, as well as species of true fir, Abies Mill. (Pinales: Pinaceae), spruces, Picea Mill. (Pinales: Pinaceae), pines, Pinus L. (Pinales: Pinaceae), and western hemlock, Tsuga heterophylla (Raf.) Sarg. (Pinales: Pinaceae), along the Pacific Slope from Alaska to California (Furniss and Carolin 1992). Both species lay eggs in roots of dying and dead trees and in logging slash in contact with the ground during adult dispersal in May. Larvae are small white grubs that excavate galleries under the root bark. Both species have a 1-yr life cycle.

In the North Central United States, Hylastes porculus Erickson (Coleoptera: Curculionidae) is a primary vector of procercum root disease, caused by Leptographium procercum (Kendrick) Wingfield (Ophiostomatales: Ophiostomataceae), in red pine (Klepzig et al. 1991). Adults are 4–5.3 mm in length (Drooz 1985). This species colonizes roots and stumps of dying pines from Maine to the Carolinas and west to the Lake States (Drooz 1985).

Hylastes salebrosus Eichhoff (Coleoptera: Curculionidae) and Hylastes tenuis Eichhoff (Coleoptera: Curculionidae) are the most common species associated with stressed, diseased, or dying pines in the southeastern United States. (Sullivan et al. 2003; Eckhardt et al. 2004; Zanzot et al. 2010). Adult H. salebrosus are about 4.5-mm long and H. tenuis about 2- to 3.5-mm long (Drooz 1985). Hylastes salebrosus occurs primarily in the south Atlantic states, whereas H. tenuis occurs over most of the United States (Drooz 1985). Both species colonize the bases and roots of stressed and dying pines and spruces (Drooz 1985).

Species of Hylurgops closely resemble Hylastes but are more robust and have a broad and bilobed third tarsal segment, whereas Hylastes have a narrow and emarginate third tarsal segment (Furniss and Carolin 1992). Adult Hylurgops are 4–5 mm long (Fig. 2; Furniss and Carolin 1992). Several species occur in the western United States (Furniss and Carolin 1992), but only Hylurgops pinifex (Fitch) (Coleoptera: Curculionidae) occurs in the East (Drooz 1985).

Several long-snouted weevils in the subfamily Molytinae also vector Leptographium root diseases. Larvae are small, nondescript, and white grubs (Fig. 3). In the West two weevils, Stereomimus carinatus (Mannerheim) (Coleoptera: Curculionidae) (Fig. 4) and Pissodes fasciatus LeConte (Coleoptera: Curculionidae), are larger, 7–10 mm in length. Adult S. carinatus and P. fasciatus are similar in shape, but S. carinatus have a rougher texture (Furniss and Carolin 1992) and are darker-colored with patches of rust-colored scales. Adult P. fasciatus are dark reddish-brown, with patches of lighter-colored scales. Stereomimus carinatus colonizes primarily Douglas-fir and Sitka spruce, Picea sitchensis (Bong.) Carr. (Pinales: Pinaceae), but also hemlock and true fir, from Alaska to Oregon (Condron 1968;
Furniss and Carolin 1992). *Pissodes fasciatus* colonizes only boles and root collars of Douglas-fir saplings from Alaska to California. Larvae of both species develop in short galleries under the bark of roots. Chip cocoons formed from wood fibers are characteristic of these weevils (Fig. 5). These species have a 1- to 2-yr life cycle (Condreshoff 1968; Furniss and Carolin 1992).

In the eastern United States, several species of *Hylobius* are the primary associates of stressed and root-diseased trees (Klepzig et al. 1991; Eckhardt et al. 2007). Adults of these species are dark reddish-brown to black with scattered patches of lighter-colored scales (Droz 1985; Furniss and Carolin 1992). In the North Central region, the pales weevil, *Hylobius pales* (Herbst) (Coleoptera: Curculionidae) (Fig. 6), the root collar weevil, *Hylobius radicus* Buchanan (Coleoptera: Curculionidae) (Fig. 7), and pitch-eating weevil, *Pachylobius picivorus* (Germar) (Coleoptera: Curculionidae) (Fig. 8), are the primary weevils associated with root-diseased red pines (Klepzig et al. 1991, 1995). In Virginia, eastern white pines, *Pinus strobus* L. (Pinales: Pinaceae) infected with procerum root disease were closely associated with the eastern pine weevil, *Pales nemorensis* Germar, and the pales weevil, with pre-emergent adults of both species found to be contaminated with the fungus (Neville and Alexander 1992). Further south, Eckhardt et al. (2007) reported that *H. pales* and *P. picivorus* were significantly associated with stressed loblolly pine in central Alabama. In the Western Gulf region, adult beetles typically emerge during late March to mid-April (Grosman et al. 1999).

Ecology

All species of root-feeding curculionids breed in dying or freshly dead roots of host conifers (Droz 1985; Furniss and Carolin 1992). All have a 1- to 2-yr life cycle. Adults typically emerge during May (Droz 1985; Witcosky et al. 1986b) and characteristically feed at the root collar of nearby seedlings (Figs. 9 and 10) prior to dispersal, girdling seedlings, and causing substantial seedling mortality (Gutzwiler 1976; Cade et al. 1981; Petersson and Örlander 2003).

Root beetles are strongly attracted to stressed, diseased, or injured host trees, especially burned or cut stands (Fox and Hill 1973; Harrington et al. 1985; Witcosky et al. 1986a,b; Klepzig et al. 1991, 1995; Hanula et al. 2002; Sullivan et al. 2003; Campbell et al. 2008). Hanula et al. (2002) and Sullivan et al. (2003) reported that...
these beetles were significantly more abundant in burned than in unburned stands. Rudinsky and Zethner-Møller (1967) reported that *H. nigrinus* is attracted to cut trees, but especially to bark beetle-killed trees. Attractiveness of cut or dying trees may persist for at least 7 mo (Witcosky et al. 1986a,b) but apparently not after 1 yr (Witcosky et al. 1986b; Sullivan et al. 2003).

In addition, several species are known to vector virulent root pathogens, particularly strains of *L. wageneri* and *L. procerum*, that cause disease and mortality in older saplings and trees (Goheen and Cobb 1978; Harrington et al. 1985; Witcosky et al. 1986a,b; Hansen and Goheen 1988; Klepzig et al. 1991, 1995; Goheen and Hansen 1993; Harrington, 1993; Schweigkofler et al. 2005). Beetles reproducing in stressed or diseased trees transmit root disease pathogens to susceptible root systems, from which the pathogen can spread to adjacent healthy root systems over short distances (Harrington 1993).

However, at least some species also can transmit fungal pathogens into apparently healthy roots. Witcosky et al. (1986a) observed adult *H. nigrinus*, in particular, wounding healthy trees by chewing on the lower stem, root collar, and proximal 50 cm of roots. Many wounds were superficial, but some beetles were recovered from tunnels penetrating to the xylem, thereby creating suitable infection courts for disease transmission. Witcosky et al. (1986a) verified that beetles transmitted the pathogen to healthy hosts under laboratory conditions. Witcosky et al. (1986a) reported that <5% of collected adult *H. nigrinus* and *S. carinatus* were contaminated with spores of *L. wageneri* but, nevertheless, were capable of transmitting the fungus into healthy, as well as cut, root systems. By comparison, Klepzig et al. (1991, 1995) reported that 7% of field-collected *Dendroctonus valens* LeConte (Coleoptera: Curculionidae) adults carried *L. procerum* spores but vectored the pathogen into 30% of wounded roots on which they were caged; 13% of field-collected *H. porculus* adults carried *L. procerum* spores but vectored the pathogen into 40% of wounded roots on which they were caged.

Attraction to injured or cut trees reflects responses to volatile compounds that are commonly emitted by stressed, diseased, or injured trees. Rudinsky and Zethner-Møller (1967) and Witcosky et al. (1987) found that *H. nigrinus* and *S. carinatus* were significantly more attracted to traps emitting ethanol or *α*-pinene than to unbaited traps and were significantly more attracted to traps baited with root sections infected with *L. wageneri* than to traps with uninfected root sections. Subsequent studies showed that these beetles generally are more strongly attracted to mixtures of ethanol and *α*- or *β*-pinene than to ethanol or pinene alone (Witcosky et al. 1987; Bedard et al. 1990; Phillips 1990; Jacobi 1992). Rieske and Raffa (1991) compared captures of *H. pales* and *P. picivorus* in pitfall traps baited with six combinations of ethanol and turpentine in a pine plantation in Wisconsin. Both species were more strongly attracted to baits containing ethanol/turpentine ratios > 1:1.

Erbilgin et al. (2001) compared captures of root- and stem-colonizing bark beetles in pitfall and lower-stem flight traps, baited with mixtures of ethanol and either (+)- or (−)-*α*-pinene, in Wisconsin and Louisiana. Root-colonizing beetles were caught primarily in pitfall traps, but stem-colonizing bark beetles were caught primarily in lower-stem flight traps. The weevils, *Hylobius* spp. (mostly *H. pales*) and *P. picivorus*, preferred (−)- over (+)-*α*-pinene in both regions, whereas the bark beetles, *H. porculus* and *D. valens*, in Wisconsin showed no preference between (+)- and (−)-*α*-pinene, in combination with ethanol. No bark beetles were caught in Louisiana (Erbilgin et al. 2001).

Other potential host attractants, such as 4-allylanisole (4AA), have been examined. Joseph et al. (2001) found that the number of most scolytid species caught in baited traps increased by 1.5-
Ixodes scapularis young plantations or native forests. This change in forest structure, that is known to be more favorable to deer and rodents than are beetles and their vectored fungi promoted early successional vegetation, suggesting attraction to bark beetle pheromones (Rudinsky and 4AA (Joseph et al. 2001).

was an exception, being significantly attracted to both low and high (Mannerheim) (Coleoptera: Curculionidae) Hylurgops subcostulatus Swaine (Coleoptera: Curculionidae), Hylastes longicollis (H. nigrinus) significantly deterred by high 4AA, including, H. rugiperatus pinifex (Fitch) (Coleoptera: Curculionidae), Hylurgops poro-gnathotrichus retusus (LeConte) (Coleoptera: Curculionidae), when compared to traps without 4AA. A high release rate of 4AA further inhibited responses for most beetles compared to low 4AA. Seven species were significantly deterred by high 4AA, including H. nigrinus, H. macer, Hylurgops reticulatus (LeConte) (Coleoptera: Curculionidae), Hylurgops poro-rubicomicus Wood (Coleoptera: Curculionidae), Hylurgops subcostulatus (Mannerheim) (Coleoptera: Curculionidae) was an exception, being significantly attracted to both low and high 4AA (Joseph et al. 2001).

Root beetles are often attracted to trees colonized by bark beetles, suggesting attraction to bark beetle pheromones (Rudinsky and Zethner-Mölle 1967). Miller et al. (2005) reported that Hylurgops rugiperatus pinifex (Fitch) (Coleoptera: Curculionidae), H. salebrosus, and H. tenuis did not respond to ipesinol, ipsdenol, or lanierone. However, H. salebrosus was attracted to the southern pine beetle, Dendroctonus frontalis Zimmerman (Coleoptera: Curculionidae) pheromone, exo-brevicomin (Phillips 1990).

Coyle et al. (2013) reported that tree mortality resulting from root beetles and their vectored fungi promoted early successional vegetation that is known to be more favorable to deer and rodents than are young plantations or native forests. This change in forest structure, in turn, increased the abundance of deer ticks, Ixodes scapularis Say (Ixodida: Ixodidae), the primary vector of Lyme disease.

Management

Prior to the 1980s, root beetles were commonly found at low densities in host stands of various ages and were generally considered to have little economic importance (Drooz 1985; Furniss and Carolin 1992). However, as landscapes in the Pacific Northwest have been transformed from dominance by diverse, older forests to young, monotypic plantations dominated by commercial species, these insects have increased in abundance and ability to kill seedlings and transmit root pathogens (Witcosky et al. 1986b; Schowalter et al. 1997; Christensen et al. 2000). In the North Central and Southern regions, efforts to protect remnant stands for biodiversity retention have led to old, unhealthy stands that have become increasingly vulnerable to a variety of root- and stem-colonizing beetles (Klepzig et al. 1991, 1995; Rieske and Raffa 1991; Eckhardt et al. 2004, 2007). The major impact of these insects in all regions is their girdling of seedlings, often devastating newly replanted stands (Gutzwiller 1976; Cade et al. 1981; Grosman et al. 1999; Taylor et al. 2006). Gutzwiller (1976) reported that S. carinatus caused 2–11% mortality to Douglas-fir seedlings in British Columbia. Cade et al. (1981) and Grosman et al. (1999) reported seedling mortality to pales weevil of 10–58% per year, depending on harvest and planting times. This level of mortality requires added expenses for control or replanting to maintain adequate seedling density.

Furthermore, species in the West and North Central regions have demonstrated ability to vector root pathogens, contributing to spread of root disease in young plantations or older forests (Harrington et al. 1985; Witcosky et al. 1986a,b; Klepzig et al. 1991, 1995). Although <13% of root beetles carry pathogen spores (Witcosky et al. 1986a,b; Klepzig et al. 1995), attraction of large numbers of beetles into susceptible stands virtually ensures establishment of new infection centers, from which root disease spreads to adjacent crop trees. Hansen and Goheen (1988) measured the rate of black-stain root disease spread over a 10-yr period in Douglas-fir plantations in Oregon and Washington. They found that tree mortality increased 4.4-fold over the 10-yr period but slowed as trees aged; all 10- to 15-yr-old trees died within 2 yr of infection, but trees >20 yr old showed greatly slowed spread of the fungus and much lower mortality rates. Overall, 31% of trees died in infection centers. Root beetles and their associated pathogens often predispose trees to tree-killing bark beetles (Goheen and Cobb 1980; Klepzig et al. 1991, 1995; Goheen and Hansen 1993; Otronska et al. 1997; Aukema et al. 2010).

Broadcast insecticides can be used as necessary to protect seedlings from emerging adults (Cade et al. 1981; Peterson and Örlander 2003; Taylor et al. 2006). Peterson and Örlander (2003) reported that Norway spruce, Picea abies (L.). (Pinales: Pinaceae), seedlings can be protected from Hypobius abietis L. (Coleoptera: Curculionidae) in Sweden by dipping in 0.75% permethrin. Taylor et al. (2006) reported that pine seedlings in the southeastern United States can be protected in the same manner. Many state forestry and private seedling companies now sell pretreated seedlings. Of course, insecticides should be used strictly according to label instructions.

Seedlings also can be protected using various barriers to root beetle colonization. Peterson and Örlander (2003) demonstrated that spraying mineral oil onto the lower portion of Norway spruce seedlings prior to planting or planting seedlings within a protective sleeve significantly reduced damage by root weevils. Given the added expense of protecting seedlings with seedling treatments, an integrated pest management approach that emphasizes preventative measures is recommended for management of these beetles. Maintaining healthy seedlings and trees and preventing attraction of root weevils to replanted stands are keys to prevention. Harvest and site preparation methods can prevent attractive conditions. Harvesting and replanting after adult beetles have dispersed, planting appropriate tree species for site conditions, providing adequate water and nutrients, and maintaining adequate spacing for optimal tree growth and...
production of chemical defenses are fundamental (Helgerson et al. 1992; Grosman et al. 1999; Schowalter 2016).

Cade et al. (1981) and Grosman et al. (1999) reported that seedling mortality to root weevils was focused in stands planted in the winter following fall harvest and site preparation. Seedling mortality was 6% in plantations established in the winter following site preparation the preceding spring, 20% following site preparation the preceding summer, and 58% following site preparation the preceding fall. Consequently, site preparation in the spring prior to winter planting is recommended. Where stands must be harvested after 1 July, planting should be delayed 1 yr. If areas harvested after 1 September must be planted the same year, then the site should be monitored intensively for root beetle activity and treated, as necessary, to reduce seedling damage.

Pettersson and Orlander (2003) tested the effect of several preventative and barrier techniques for minimizing damage to Norway spruce seedlings in Sweden. They found that shelterwood harvest (compared to clearcutting), soil scarification (litter removal to bare soil), and physical protection (barriers to root beetle feeding) were additive. A combination of these three methods reduced girdling to <7% of seedlings after 3 yr, compared to 88% of unprotected seedlings on clearcuts with no soil scarification. The effectiveness of individual treatments for reducing root weevil damage was insecticide (permethrin) > soil scarification > physical protection > shelterwood harvest. Soil scarification reduced damage equally well on clearcuts and shelterwoods, but effects lasted longer in shelterwood treatments. Similarly, Grosman et al. (1999) reported that seedling mortality due to pales weevil feeding decreased with increasing intensity of site preparation.

Precommercial thinning and prescribed fire are two management tools used to reduce competition, control stand density, and enhance growth of crop trees (Tesch and Tappeiner 1992). However, fire can injure crop trees and attract root beetles (Hanula et al. 2002; Sullivan et al. 2003). Sullivan et al. (2003) recommended that prescribed fire should be conducted in a way that prevents fire penetration into the duff layers, e.g., dormant-season heading fires performed under adequate moisture conditions to permit elimination of litter fuels without injuring pine roots. Sells et al. (2013) reported that fire treatments conducted in this way to control cogongrass, Imperata cylindrica (L.) P. Beav. (Poales: Poaceae), did not result in elevated root beetle abundances.

Precommercial or commercial thinning is also an effective means to reduce stand competition and vulnerability to stem-colonizing bark beetles (Schowalter and Turchin 1993; Schowalter 2012). However, Harrington et al. (1985) and Witcosky et al. (1986a,b) demonstrated that root beetles are attracted to thinned stands for up to a year. The timing of thinning can be manipulated to provide the benefits of thinning without inducing problems with root beetles, as described in the next paragraph.

Thinning, and perhaps fire, creates stumps that emit host terpenes and other host volatiles including, as they decay, ethanol, a combination that is highly attractive to root beetles (Witcosky et al. 1987, Sullivan et al. 2003). Witcosky et al. (1986a,b) found that stands thinned during the previous fall and winter attracted significantly more beetles dispersing in May than did stands thinned during May or unthinned (Fig. 11). The numbers of H. nigrius were 70-fold higher in stands thinned the previous September, >100-fold higher in stands thinned the previous January, and 20-fold higher in stands thinned during the current May, compared to unthinned controls. The incidence of root beetle galleries in crop trees was 11% higher for September thinning, 17% higher for January thinning, and 5% higher for May thinning, compared to unthinned controls. Although <5% of beetles were contaminated by L. wageneri spores, the elevated abundances of beetles in thinned stands virtually ensured transmission of root pathogens to crop trees. Witcosky et al. (1986b) suggested that thinning should be avoided in areas of high risk for black-stain root disease or, if thinning is necessary, it should be implemented during June or July following beetle dispersal in May. Thinning during this time period also should reduce damage by bark beetles.

Attractive semiochemicals can be used to monitor abundances of these species. A bait consisting of ethanol plus (−)-α-pinene provides particularly effective attraction for trapping purposes (Witcosky et al. 1987; Miller and Rabaglia 2009). Miller and Duerr (2008) compared trap catches with wet collecting cups (containing 25–30% propylene glycol as killing agent) or dry collecting cups (containing a dichlorvos-impregnated wax bar as killing agent) and concluded that wet cups are more effective for most species, especially at low population densities when detection is most critical.

Unfortunately, despite the apparent attractiveness of lures containing α-pinene and ethanol, root beetle behavior and abundances have not been manipulated successfully (e.g., mass trapping or population displacement). Verbenone, used to repel some stem-colonizing bark beetles, was not effective when tested on H. longicollis and H. porosus and is not recommended for management of root beetles (Lindgren and Miller 2002).

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References Cited

Aukema, B. H., J. Zhu, J. Moller, J. G. Rasmussen, and K. F. Raffa. 2010. Predisposition to bark beetle attack by root herbivores and associated pathogens: roles in forest decline, gap formation, and persistence of endemic bark beetle populations. For. Ecol. Manage. 259: 374–382.

Bedard, W. D., G. T. Ferrell, M. C. Whitmore, and A. S. Robertson. 1990. Trapping evaluation of beetle vectors of black stain root disease in Douglas-fir. Can. Entomol. 122: 459–468.

Fig. 11. Mean abundance of H. nigrius in unthinned, 12-yr-old plantations (black squares) of Douglas-fir and plantations thinned in September 1982 (asterisks), January 1983 (black circles), or May 1983 (white circles) in western Oregon. Arrow indicates time of thinning in May 1983. From Witcosky et al. (1986b), courtesy of the Research Council of Canada.
Schowalter, T. D., E. M. Hansen, R. Molina, and Y. Zhang. 1997. Integrating the ecological roles of phytophagous insects, plant pathogens, and mycorrhizae in managed forests, pp. 171–189. In K. A. Kohm and J. F. Franklin (eds.), Creating a forestry for the 21st century. Island Press, Washington, DC.

Schweigkofler, W., W. J. Otrosina, S. L. Smith, D. R. Chock, K. Maeda, K. G. Peay, and M. Garbelotto. 2005. Detection and quantification of Leptographium wageneri, the cause of black-stain root disease, from bark beetles (Coleoptera: Scolytidae) in Northern California using regular and real-time PCR. Can. J. For. Res. 35: 1798–1808.

Sells, S. M., D. W. Held, S. F. Enloe, N. J. Loewenstein, and L. G. Eckhardt. 2013. Impact of cogongrass management strategies on generalist predators in cogongrass-infested longleaf pine plantations. Pest Manag. Sci. 71: 478–484.

Sullivan, B. T., C. J. Fettig, W. J. Otrosina, M. J. Dalusky, and C. W. Berisford. 2003. Association between severity of prescribed burns and subsequent activity of conifer-infesting beetles in stands of longleaf pine. For. Ecol. Manage. 185: 327–340.

Taylor, E. L., A. G. Holley, and M. Blazier. 2006. New pine planting strategies for the western Gulf states. Southern regional extension forestry technology bulletin SREF-FM-003. Texas Cooperative Extension, College Station, TX. file:///C:/Users/tschowalter/Downloads/New%20Pine%20Planting%20Strategies%20for%20the%20Western%20Gulf%20States.pdf (accessed 26 March 2018).

Tesch, S. D., and J. C. Tappeiner II. 1992. Planning for reforestation success, pp. 2–25. In S. D. Hobbs, S. D. Tesch, P. W. Owston, R. E. Stewart, J. C. Tappeiner II, and G. E. Wells (eds.), Reforestation Practices in Southwestern Oregon and Northern California. Forest Research Laboratory, Oregon State University, Corvallis, OR.

Witcosky, J. J., T. D. Schowalter, and E. M. Hansen. 1986a. Hylastes nigrinus (Coleoptera~ Scolytidae), Pissodes fasciatus, and Steremnius carinatus (Coleoptera: Curculionidae) as vectors of black-stain root disease of Douglas-fir. Environ. Entomol. 15: 1090–1095.

Witcosky, J. J., T. D. Schowalter, and E. M. Hansen. 1986b. The influence of time of precommercial thinning on the colonization of Douglas-fir by three species of root-colonizing insects. Can. J. For. Res. 16: 745–749.

Witcosky, J. J., T. D. Schowalter, and E. M. Hansen. 1987. Host-derived attractants for the beetles, Hylastes nigrinus (Coleoptera: Scolytidae) and Steremnius carinatus (Coleoptera: Curculionidae). Environ. Entomol. 16:1310–1313.

Zanzot, J. W., G. Matusick, and L. G. Eckhardt. 2010. Ecology of root-feeding beetles and their associated fungi on longleaf pine in Georgia. Environ. Entomol. 39: 415–423.

Zeng, Y., K. R. Kidd, and L. G. Eckhardt. 2014. The effect of thinning and clear-cut on changes in the relative abundance of root-feeding beetle (Coleoptera: Curculionidae) in Pinus taeda plantations in central Alabama and Georgia. Pest Manag. Sci. 70: 915–921.

Zethner-Møller, O., and J. A. Rudinsky. 1967. On the biology of Hylastes nigrinus (Coleoptera: Scolytidae) in western Oregon. Can. Entomol. 99: 897–911.