Host Interactions of the Balsam Woolly Adelgid

Leslie P. Newton and Fred P. Hain

Department of Entomology, College of Agriculture and Life Sciences,
North Carolina State University, Raleigh, NC 27695

ABSTRACT

The balsam woolly adelgid (BWA), *Adelges piceae* Ratz., has caused immense damage to native and planted fir stands for the past century. This paper highlights the current understanding of the initiation of damage by the insect and the host responses to the insect. Although most native North American firs (*Abies* spp.) are highly susceptible to the adelgid, other firs exhibit a range of resistance and some can tolerate even heavy infestations. Possible mechanisms for resistance are discussed.

INTRODUCTION

The balsam woolly adelgid (BWA), *Adelges piceae* Ratz. (Hemiptera: Adelgidae), an inconspicuous insect that feeds on true firs, has caused considerable damage in North American fir stands for the last century. Native stands of mature Fraser fir (*Abies fraseri* [Pursh] Poir.) in the southern Appalachians have come close to elimination (Dull et al. 1988), and the adelgid has altered the composition of the surviving stands (Jenkins 2003). The balsam fir (*Abies balsamea* [Linn.] Mill.) forests of New England and Canada and the mixed fir forests of the Pacific Northwest have been continually plagued by the insect for almost 100 years and the natural stands of Fraser fir in the Southern Appalachians for over 50 years. Grand fir (*Abies grandis* [Dougl.] Lindl.) is gradually being eliminated from low elevation landscapes in the Pacific Northwest and subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) is being removed as a pioneer tree species in the Cascades (Mitchell and Buffam 2001).

Accidentally introduced into Maine and Nova Scotia around the turn of the 20th Century, (Balch 1952), most likely on imported nursery stock of European silver fir (*Abies alba* Mill.), BWA had become established on balsam fir in Maine by 1908 (Kotinsky 1916). The adelgid was first reported on Fraser fir in the Southern Appalachians on Mount Mitchell in 1957 (Speers 1958) and quickly spread throughout the natural range of Fraser fir. On the West Coast, it was first reported on ornamental firs near San Francisco (Annand 1928). In the Pacific Northwest, it was first reported on grand fir in the Willamette Valley of Oregon (Keen 1952). There, the most frequent hosts are Pacific silver fir (*A. amabilis* [Dougl.] Forbes) and subalpine fir at high elevations and grand fir in valleys (Mitchell et al. 1961). The adelgid was reported in British Columbia on Pacific silver fir and on Vancouver Island on grand fir by the late 1950s (Silver 1959).

SUBSPECIES OF THE BWA

Three geographic subspecies of *A. piceae* Ratz. have been identified in North America (Foottit and Mackauer 1983). *Adelges piceae piceae* (Ratzeburg 1844) has been observed in British Columbia, the Pacific Northwest, and in the native Fraser fir range in the Southern Appalachians. This subspecies corresponds morphologically to Pschorn-Walcher and Zwolfer's *forma typica* (1956) and the 'intermediate group' of Foottit and Mackauer (1980). *Adelges piceae canadensis* (Merker and Eichhorn 1956) is found on balsam fir in Quebec and the maritime provinces of Canada, and in the northeastern United States. *Adelges piceae occidentalis*, subsp. nov. has been observed on Pacific silver fir and grand fir in British Columbia and may be the result of a single introduction. The subspecies are based on the morphological differences of first instars and adults between the three subspecies (*e.g.*, body shape, length, dorsal plates, fusion of pleural and mesial plates, shape of pore fields of mesial plates, number and range of wax pores, etc.).

LIFE HISTORY OF *ADELGES PICEAE*

In North America, *A. piceae* exhibits an anholocyclic mode of generation on fir and does not migrate to spruce (*Picea*), as it does in its native range. The sistens form is wingless and develops on the stem (lenticels, crevices in bark, or callus tissue), branches, or bases of buds (Crystal 1925, Balch 1952). The number of sistens generations per year depends upon temperature and host condition. There is only one hiemosistens generation per year and as many as three or four aestivosistens generations. The sistens—both hiemosistens and aestivosistens—develop through four stages after emerging from the egg: first instar (crawler, neosistens), second and third instar, and adult. The progrediens form, which never overwinters and rarely enters into any period of diapause, can be wingless (aptera) or winged (alata) and develops on the needles of fir (Crystal 1925, Balch 1952, Varty 1956). The progrediens form, observed only in the subspecies *A. piceae canadensis* in North America (Foottit and MacKauer 1983), arises from the first eggs laid by the hiemosistens, differs morphologically from the sistens, and has a shorter embryonic developmental period than the sistens (Eichhorn 1969).

INITIATION OF DAMAGE TO INDIVIDUAL TREES

Balch (1952) described the process of feeding, a summary of which follows. *Adelges piceae* has piercing-sucking mouthparts (stylets) and feeds on parenchyma tissue within the outer 1.5 mm of bark or on twigs at the base of buds. The stylets are inserted through the phellem (epidermis) into the phelloderm (cortex), probing between cells, until a suitable feeding site can be located. Salivary secretions, which can flow into intercellular spaces, are exuded from the tip of the maxillae to form a sheath that lines the path of the stylets. The neosistens inserts its stylets full length before entering diapause. Feeding occurs through repeated partial withdrawal and reinsertion of the stylets in a new direction. The stylets are withdrawn and completely renewed at each molt, with the new stylets inserted near the original point of entry.

The tracks are branched and affect tissue in a 360° pattern. Aphids feed in a similar pattern and are able to assess feeding sites by intermittently ejecting and sucking back up a watery saliva along with soluble material from the host; this watery saliva is diffused into surrounding tissue and can be transported within the host plant (Miles 1965 and 1999). Because of the close relationship between aphids and adelgids, and the many similarities in feeding patterns and capabilities, it is likely that adelgids also secrete the watery saliva, which is then transported through the tree.

The adelgid's salivary secretions appear to create a chemical imbalance within the tree and disrupt the development of normal tissue. Auxin-like compounds (Balch et al. 1964) and pectinase (Adams and McAllan 1958, Forbes and Mullick 1970) have been found in adelgid saliva. Additionally, the gel-like stylet sheath may often form a barrier around damaged parts of parenchyma cells, preventing the disintegration and rupture of cell vacuoles, which would normally be followed by the production of autotoxic defensive compounds in surrounding cells (Miles 1999). The stylet sheath can also slow down or prevent the production of the phenolics that arise from and promote necrosis by adsorbing and immobilizing the phenolics (Miles 1999).

RESPONSE OF *ABIES* SPECIES TO *ADELGES PICEAE* ATTACK

All *Abies* species are susceptible, in varying degrees, to some species of adelgid throughout the world, and susceptibility to *A. piceae* attack varies widely. Firs native to North America (subalpine fir, balsam fir, and Fraser fir) are highly susceptible. Some western species (grand fir, sacred fir [*Abies religiosa* (H.B.K.) Schlecht. et Cham], and noble fir [*Abies procera* Rehd.]) and firs native to central Europe tolerate infestation (Varty 1956, Mitchell 1966), while some Asian species (Veitch fir [*Abies veitchii* Lindl.] and Momi fir [*Abies firma* Sieb. et Zucc.]) appear to be immune to attack, at least in North America (Hall et al. 1971).

Adelgid infestations follow a general trend. The initial infestation begins with a few large trees, generally with deep fissures, and then spreads to nearby trees. The population peaks and when many trees have been killed or are damaged, the population diminishes. This second period may go on for an indefinite period of time and is characterized by increasing gout and gradual dying of trees. Some trees may nevertheless recover. The first outbreak is generally the most severe (Balch 1952), but the infestations can persist for decades, and many stands are gradually succumbing to the stress (Mitchell and Buffam 2001). Stem attack is generally observed in continental climatic zones and twig attack in maritime zones (Greenbank 1970, Schooley and Bryant 1978). Mass stem infestations can cause tree mortality within two to three years. With a crown infestation, the tree will suffer branch dieback and general deterioration, and it can take as long as 10 to 20 years for mortality to occur (Bryant 1974).

Some species exhibit a 'bottom-up' pattern of infestation, wherein the infestation begins on the lower portion of the stem and works upwards towards the crown over time (e.g., in grand fir [Mitchell 1966] and Fraser fir [Amman and Talerico 1967]). Others exhibit a 'top-down' pattern, with the infestations beginning in the crown and working downward (e.g., in balsam fir [Greenbank 1970]). All ages of fir in plantations are susceptible, particularly with

Fraser fir, while in natural stands, older, mature trees are more susceptible. This begs the question as to whether there is something in younger trees—physical or chemical—that protects them from severe infestations.

Infestations are generally classified as "stem" or "crown" infestations. The damage, both microscopic and macroscopic, is fairly consistent among all susceptible firs. With a crown infestation, gouting is apparent. Growth of wood and bark is stimulated at the point of stylets insertion and both hypertrophy and hyperplasia occur. An enlargement of parenchyma cells (up to six or seven times the size of normal cells), including cell walls and nuclei, occurs and these large cells are continually produced, causing swelling of the twigs and in the bark (Balch 1952). Pock-like swellings are often observed on the bark of young trees (Rudinsky 1956). The number of rays increase (Doerksen and Mitchell 1965), as do the number of parenchyma strands (Smith 1967). Large reductions in carbohydrate reserves of needles and twigs have been observed (Puritch and Talmon-De L'Armee 1971). Increasing numbers of these enlarged parenchyma cells disrupt the phloem channels and interfere with the metabolic pathways in the bark (Bryant 1971). Bud growth often ceases and the twig begins to die back from the ends—a flattened top is often observed in infested trees (Balch 1952, Mitchell 1967). In fact, this loss of apical dominance (observed in stem infestations as well as crown infestations) is often the first symptom looked for in Fraser fir Christmas tree plantations when scouting for *A. piceae* infestation (Sidebottom 2004). In addition to gouting, the number and length of branches and the length of the stem are often reduced in a crown infestation (Balch 1952, Schooley 1974).

With a stem infestation, although the stylets of the adelgid can be up to 5 mm from the vascular cambium, xylem production is often compromised resulting in abnormal wood called 'rotholz' or 'redwood'. Rotholz is anatomically similar to compression wood in conifers (Balch 1952). These resultant tracheids are circular rather than rectangular (Timell 1986); are short, thick walled, and highly lignified with small lumens (Doerksen and Mitchell 1965); have a reduced number of conducting pits (Puritch and Petty 1971), higher specific gravity, and greater fibril angle (Foulger 1968); and often have encrusted pit membranes such as those found in heartwood (Puritch and Johnson 1971). Traumatic resin ducts may form in the xylem (Saigo 1976). Sapwood permeability in grand fir has been reduced to 5% of that of normal sapwood (Puritch 1971). Ultimately, these changes throw the tree into physiological drought, reducing the flow of water within the tree and compromising photosynthesis, transpiration, and respiration (Puritch 1973). Heavy infestations can result in tree mortality in one to two years (Balch 1952). Adelgid infestation appears to contribute to premature heartwood formation (Puritch 1977). Rotholz production has also been associated with a significant increase in the proportional area of heartwood (Hollingsworth et al. 1991) and higher percentages of latewood (Doerksen and Mitchell 1965, Smith 1967).

The changes that take place in the bark of the fir trees initially create a more favorable environment for adelgid development, and in the early stages of an infestation fecundity is at its peak; as the trees weaken and the population begins to dwindle, fecundity also decreases (Pschorn-Walcher and Zwolfer 1958, Amman 1970).

HOST RESPONSES THAT MAY AID IN RESISTANCE

Some responses to adelgid attack may aid in the resistance or tolerance to infestation. Many conifers have the ability to form a secondary periderm, consisting of necrophylactic tissue, around a wound (Mullick 1975, Hain et al. 1991). This wound healing mechanism can isolate an area of bark occupied by the adelgid and can effectively protect the underlying bark from further attack for years (Balch 1952, Mullick 1971). It has been hypothesized that the formation of the protective secondary periderm may be inhibited or compromised by chemicals secreted by the adelgid's stylets (Mullick 1975, 1977), though subsequent research has both supported (Hay and Eagar 1981) and failed to support (Arthur and Hain 1985) this hypothesis.

Juvabione or juvabione-like compounds may be produced in response to adelgid attack, as has been evidenced in grand fir and Pacific silver fir (Puritch and Nijholt 1974) and Fraser fir (Fowler et al. 2001). Juvabione-like compounds, which were first discovered in 1965—the famous 'paper factor' of Slama and Williams (1965) isolated from paper towels produced from balsam fir fiber (most likely adelgid-infested balsam fir)—mimic insect juvenile hormones and have been shown to inhibit or disrupt normal development in a number of insects, including *A. piceae* (Fowler 1999). It is possible that, in mature firs that exhibit some resistance or tolerance to BWA, there is a rapid accumulation of chemicals (monoterpenes and juvabione-like sesquiterpenoids) at the site of attack that may interfere with adelgid development. Younger trees or seedlings may be protected by a naturally high accumulation of juvabione-related compounds.

Some firs, particularly grand fir, produce copious amounts of resin in response to wounds. This may serve as a means of resistance, as grand fir is one of the more resistant species of American firs, with only 20-30% mortality associated with adelgid infestation (Mitchell 1966). Many conifers have evolved resin-based defenses, such as oleoresin—a mixture of terpenoids consisting of a terpentine and rosin fraction—to deter insect pests and their symbiotic fungal pathogens. True firs store only small amounts of primary resin in bark blisters, but respond to wounding by producing oleoresins in nonspecialized, adjacent tissues. But increased resin production may be only a short-term solution to BWA. For example, in *A. grandis*, after two to five years of adelgid feeding, a portion of bark below the surface dies, the bark turns black, and this is accompanied by a heavy resin flow. This discourages further attack, but after a few years, the resin hardens and the bark develops fissures, whereupon the adelgids are able to reinfest the same areas (Mitchell 1966).

OTHER FACTORS THAT MAY AID RESISTANCE

The onset of water stress (physiological drought), one of the chief factors in susceptibility to damage, differs among fir species, and those exhibiting a more rapid onset are more susceptible to intense damage (Varty 1956, Mitchell 1967). It follows that species or individual trees within a species that exhibit high levels of drought resistance would also be more resistant or tolerant of BWA.

Production of thick outer bark, as found in European silver fir, has been associated with resistance to or recovery from adelgid attack (Pschorn-Walcher and Zwolfer 1958, Schooley and Bryant 1978).

The texture of the bark may also be an important factor in resistance or susceptibility. Rough or flaky bark may be more preferable for *A. piceae* for a number of reasons, including the interception of airborne eggs and crawlers, stereotropism (the insect is stimulated to grow or change in response to touch), and more easily accessible nutritive areas (*e.g.*, lenticels and bark crannies) composed of young parenchyma (Varty 1956). In fact, lenticel development has been observed to be 'the best single predictor' for BWA population levels on Fraser fir in the Great Smoky Mountains (Hay and Eagar 1981).

Some provenances of Fraser fir appear to respond to adelgid infestation differently than others. For example, BWA infestation was not discovered on Mount Rogers until 1979, although there was evidence that some trees had been under attack for up to 17 years (Haneman et al. 1981), and high mortality was not observed until the 1990s. Mount Rogers' trees become heavily infested but do not appear to suffer rapid mortality (Hollingsworth and Hain 1991, Nicholas et al. 1992). The fir trees on Mount Rogers have been shown to be genetically different (unique allele frequencies) from other natural populations of Fraser fir (Ross 1988), but these differences have not been correlated with susceptibility to adelgid infestation (Hain et al. 1991). Nonetheless, Mount Rogers trees have been shown to form lower levels of rotholz and higher levels of secondary periderm in response to adelgid attack when compared to trees from Mount Mitchell (Hollingsworth and Hain 1992). It has been suggested that these trees may possess the ability to develop secondary periderm more rapidly than those in other locations—this characteristic may aid in adelgid tolerance (Hay and Eagar 1981). Additionally, the trees on Mount Rogers may be less likely to suffer water stress when infested partly due to environmental factors (deep soil, little wind) (Hollingsworth and Hain 1994).

Within the natural range of Fraser fir, although the majority of mature fir trees have been killed, there are remnant populations that have survived multiple decades of adelgid attack. It remains to be seen as to whether these trees have survived as a result of genetic resistance or whether the environment (most are at the highest elevations) plays a more important role.

Among and within all *Abies* species, even those highly susceptible to BWA, trees have been observed time and again to tolerate and even recover from adelgid attack. It is not an uncommon occurrence for balsam fir to recover from adelgid attack after a few years with a replacement of the original leaders and relatively small stem deformities from gouting (Balch and Carroll 1956, Schooley 1976, Schooley and Bryant 1978). Although Mount Mitchell Fraser firs suffered high mortality during the initial wave of infestation, have been shown to be highly susceptible to adelgid damage (Dull et al. 1988), and individual trees cored at Mount Mitchell showed production of rotholz at some point, the trees were uninfested and otherwise appeared healthy (Hain et al. 1991).

CONTINUING THE RESEARCH

Much of the current research focuses on understanding interactions between adelgid, host tree, and the environment. Putative genetic resistance—even within a highly susceptible species such as Fraser fir—is believed to exist, and studies are underway to begin the process of screening across and within *Abies* species for host resistance to BWA. Bark and wood chemicals associated with resistance are being isolated, and studies into the genetic components of resistance continue. The adelgid itself continues to be studied and a method of artificially rearing the insect is currently being developed. Biological control continues to be an area of interest, particularly in Christmas tree plantations at lower elevations.

Balsam woolly adelgid research is as critical now as ever. The insect is a tremendous problem in Christmas tree plantations and costs growers thousands upon thousands of dollars each year. Native stands of Fraser fir exist only in small island populations at the highest elevations in southern Virginia, western North Carolina and eastern Tennessee. Most mature trees were killed during the initial phase of adelgid infestation, but fortunately, many areas were repopulated with young natural seedlings. These regenerated stands have now reached the age wherein they become more susceptible to adelgid attack. The adelgids have continued to exist at low levels in the native stands, and the question arises as to whether the regenerated firs are more resistant to the adelgid than their predecessors. Adelgid populations should be evaluated to determine whether they are increasing, and the compounding effects of air pollution on the physiology of both tree and adelgid should be further assessed.

Researchers continue to delve into the interactions between the balsam woolly adelgid and its host species, advancing the understanding of both insect and host genetics and physiology. The hope remains that host resistance mechanisms can be identified and that, between the inherent resistance in some trees and the breeding or nurturing of resistance in others, the balsam woolly adelgid can be better tolerated in plantations and natural stands and that Fraser fir will remain an important component in the high elevation ecosystems of the Southern Appalachians.

REFERENCES

Adams, J.B. and J.W. McAllan. 1958. Pectinase in certain insects. *Canadian Journal of Zoology* 36: 305-308.

Amman, G.D. and R.L. Talerico. 1967. Symptoms of infestation by the balsam woolly aphid displayed by Fraser fir and bracted balsam fir. USDA Forest Service Research Note SE-85. 4 p.

Amman, G.D. 1970. Phenomena of *Adelges piceae* populations (Homoptera: Phylloxeridae) in North Carolina. *Annals of the Entomological Society of America* 63(6):1727-1734.

Annand, P.W. 1928. A Contribution Toward a Monograph of the Adelgidae (Phylloxeridae) of North America. Stanford University Press, Palo Alto, California. 146 p.

Arthur, F.H. and F.P. Hain. 1985. Effects of selected chemicals on non-suberized impervious tissue (NIT) formation in Fraser fir. *Journal of Entomological Science* 20(3):305-311.

Balch, R.E. 1952. Studies of the balsam woolly aphid, *Adelges piceae* (Ratz.) and its effect on balsam fir, *Abies balsamea* (L.) Mill. Canadian Department of Agriculture Publication 867. 76 p.

Balch, R.E. and W.J. Carroll. 1956. The balsam woolly aphid. Canadian Department of Agriculture, Forest Biology Division, Publication 977. 7 p.

Balch, R.E., J. Clarke, and J.M. Bonga. 1964. Hormonal action in products of tumors and compression wood (in *Abies balsamea*) by an aphid (*Adelges piceae*). *Nature* 202:721-722.

Bryant, D.G. 1974. A review of the taxonomy, biology and importance of the adelgid pests of true firs. Canadian Forest Service, Newfoundland Forest Research Centre, Information Report N-X-111. 50 p.

Bryant, D.G. 1971. Balsam woolly aphid *Adelges piceae* (Homoptera: Phylloxeridae) seasonal and spatial development in crowns of balsam fir, *Abies balsamea*. *Canadian Entomologist* 103:1411-1420.

Crystal. 1925. The genus *Dreyfusia* in Britain and its relation to the Silver fir. Phil. Trans. London Roy. Soc., Ser. B., CCXIV:29-61.

Doerksen, A.H. and R.G. Mitchell. 1965. Effects of the balsam woolly aphid upon wood anatomy of some western true firs. *Forest Science* 11:181-188.

Dull, C.W., J.D. Ward, H.D. Brown, G.W. Bryan, W.H. Clerke, and R.J. Uhler. 1988. Evaluation of spruce and fir mortality in the Southern Appalachian mountains. USDA Forest Service Southern Region Protection Report R8-PR 13.

Eichhorn, O. 1969. Problems of the determination of morphs in the genus *Dreyfusia* C.B. (Homoptera: Adelgidae), p. 437-446. *In* Proceedings of the 148th Annual Meeting of the Suisse Society of Natural Sciences in Einsiedeln (Sept. 27-29, 1969).

Foottit, R.G. and Mackauer, M. 1983. Subspecies of the balsam woolly aphid, *Adelges piceae* (Homoptera: Adelgidae), in North America. *Ann. Entomol. Soc. Am.* 7:299-304.

Foottit, R.G. and M. Mackauer. 1980. Morphometric variation between populations of the balsam woolly aphid, *Adelges piceae* (Ratzeburg) (Homoptera: Adelgidae), in North America. *Can. J. Zool.* 58:1494-1503.

Forbes, A.R. and D.B. Mullick. 1970. The stylets of the balsam woolly aphid, *Adelges piceae* (Homoptera: Adelgidae). *The Canadian Entomologist* 102:1074-1082.

Foulger, A.N. 1968. Effect of aphid infestation on properties of grand fir. *Forest Products Journal* 18(1): 43-47.

Fowler, G. 1999. The Potential of Juvabione as a Host Resistance Mechanism against the Balsam Woolly Adelgid (*Adelges piceae* [Ratzeburg]). Ph.D. Dissertation, North Carolina State University Department of Entomology. 118 p.

Fowler, G., J. Zhang, F.P. Hain, and J.F. Manville. 2001. The distribution pattern of two juvenile hormone related compounds in Fraser fir and the induced response to a balsam woolly adelgid infestation. *Canadian Journal of Forest Research* 31(10):1701-1707.

Greenbank, D.O. 1970. Climate and the ecology of the balsam woolly aphid. *The Canadian Entomologist* 102:546-578.

Hain, F.P., R.G. Hollingsworth, F.H. Arthur, F. Sanchez, and R.K. Ross. 1991. Adelgid host interactions with special reference to the balsam woolly adelgid in North America. *In* Forest Insect Guilds: Patterns of Interaction with Host Trees, ed. Y.N. Baranchikov, W.J. Mattson, F.P. Hain, and T.L. Payne. U.S. Dept. Agric. For. Serv. Gen. Tech. Rep. NE-153: 271-287.

Hall, J., P. Singh, and H.O. Schooley. 1971. Survival and growth of some exotic firs in Newfoundland. *For. Chron.* 47:279-291.

Haneman, D.M., H.L. Lambert, and D.D. Johnston. 1981. Detection and evaluation of the balsam woolly aphid infestations on Mount Rogers, Virginia, 1980. Forest Insect and Disease Management (US Forest Service, Southeast), Report #81-1-12.

Hay, R.L. and C. Eagar. 1981. Stem morphology and physiology of Fraser fir in relation to balsam woolly aphid attack preference. Final Contract Report for Regional Chief Scientist, Southeast Regional Office, National Park Service. 60 p.

Hollingsworth, R.G. and F.P. Hain. 1991. Balsam woolly adelgid (Homoptera: Adelgidae) and spruce-fir decline in the Southern Appalachians: assessing pest relevance in a damaged ecosystem. *Florida Entomologist* 74(2):179-187.

Hollingworth, R.G. and F.P. Hain. 1992. Balsam woolly adeglid (Homoptera: Adelgidae) effects on wood and bark structure of Fraser fir and silver fir. *Environ. Entomol.* 21(5):1103-1109.

Hollingsworth, R.G. and F.P. Hain. 1994. Effect of drought stress and infestation by the balsam woolly adelgid (Homoptera: Adelgidae) on abnormal wood production in Fraser fir. *Can. J. For. Res.* 24:2295-2297.

Hollingsworth, R.G., U. Blum, and F.P. Hain. 1991. The effect of adelgid-altered wood on sapwood conductance of Fraser fir Christmas trees. IAWA (Int. Assoc. Wood Anat.) Bull. New Ser. 12: 235-239.

Jenkins, M.A. 2003. Impact of the balsam woolly adelgid (*Adelges piceae* Ratz.) on an *Abies fraseri* (Pursh) Poir. dominated stand near the summit of Mount LeConte, Tennessee. *Castanea* 68(2): 109-118.

Keen, F.P. 1952. Insect enemies of western forests. USDA Misc. Pub. 273 (revised). Washington, D.C. 280 p.

Kotinsky, J. 1916. The European fir trunk louse, *Chermes* (*Dreyfusia*) *piceaea* Ratz. Proc. Entomol.Soc. Wash. 18: 14-16.

Merker, E. and O. Eichhorn. 1956. (Grouping in the genus *Adelges*.) *Die Naturwissenschaften* 43: 453-454. (In German.)

Miles, P.W. 1965. Studies on the salivary physiology of plant-bugs: the saliva of aphids. *Journal of Insect Physiology* 11:1261-1268.

Miles, P.W. 1999. Aphid saliva. *Biol. Review* 74:41-85. Cambridge Philosophical Society.

Mitchell, R.G., N.E. Johnson and J.A. Rudinsky. 1961. Seasonal history of the balsam woolly aphid (*Adelges piceae*) in the Pacific Northwest. *Can. Ent.* 93:794-798.

Mitchell, R.G. 1966. Infestation characteristics of the balsam woolly aphid in the Pacific Northwest. U.S. Dept. Agric. Serv. Res. Pap. PNW-35. 18 p.

Mitchell, R.G. 1967. Translocation of dye in grand and subalpine firs infested by the balsam woolly adelgid. USDA Forest Service Research Note PNW-46. 17 p.

Mitchell, R.G. and P.E. Buffam. 2001. Patterns of long-term balsam woolly adelgid infestations and effects in Oregon and Washington. *Western Journal of Applied Forestry* 16(3):121-126.

Mullick, D.B. 1971. Natural pigment differences distinguish first and sequent periderms of conifers through a cryofixation and chemical techniques. *Canadian Journal of Botany* 49:1703-1711.

Mullick, D.B. 1975. A new tissue essential to necrophylactic periderm formation in the bark of four conifers. *Canadian Journal of Botany* 53(21):2443-2457.

Mullick, D.B. 1977. The non-specific nature of defense in bark and wood during wounding, insect and pathogen attack, pp. 395-441. *In* Recent Advances in Phytochemistry, Vol. 11, ed. F.A. Loewus and V.C. Runeckles. New York: Plenum Publishing.

Nicholas, N.S., S.M. Zedaker, and C. Eagar. 1992. A comparison of overstory community structure in 3 Southern Appalachian spruce-fir forests. *Bulletin of the Torrey Botanical Club* 119(3):316-332.

Pschorn-Walcher, H. and H. Zwölfer. 1956. The predator complex of the white-fir woolly aphids. (*Dreyfusia*: Adelgidae). *Zeitschrift fur Angewandte Entomologie* 39:63-75.

Pschorn-Walcher, H. and H. Zwölfer. 1958. Preliminary investigations on the *Adelges* populations (Hemiptera: Adelgidae) living on the trunk of the silver fir. *Zeitschrift fur Angewandte Entomologie* 42:241-277. (In German.)

Puritch, G.S. 1971. Water permeability of the wood of grand fir (*Abies grandis* [Doug.] Lindl.) in relation to infestation by the balsam woolly aphid *Adelges piceae* (Ratz.). *J. Exptl. Bot.* 22:936-45.

Puritch, G.S. 1973. Effect of water stress on photosynthesis, respiration and transpiration of four *Abies* species. *Can. J. For. Res.* 3:293-298.

Puritch, G.S. 1977. Distribution and phenolic composition of sapwood and heartwood in *Abies grandis* and the effects of the balsam woolly aphid. *Canadian Journal of Forest Research* 7(1):54-62.

Puritch, G.S. and R.P.C. Johnson. 1971. Effects of infestation by the balsam woolly aphid, *Adelges piceae* (Ratz.) on the ultrastructure of bordered-pit membranes of grand fir, *Abies grandis* (Doug.) Lindl. *J. Exp. Bot.* 22:953-958.

Puritch, G.S. and W.W. Nijholt. 1974. Occurrence of juvabione-related compounds in grand fir and Pacific silver fir infested by balsam woolly aphid. *Can. J. Bot.* 52:585-587.

Puritch, G.S. and J.A. Petty. 1971. Effect of balsam woolly aphid, *Adelges piceae* (Ratz.), infestation on the xylem of *Abies grandis* (Doug.) Lindl. *J. Exp. Bot.* 22:946-952.

Puritch, G.S. and M. Talmon-De L'Armee. 1971. Effect of balsam woolly aphid, *Adelges piceae*, infestation on the food reserves of grand fir, *Abies grandis*. *Can. J. Bot.* 49:1219-1223.

Ross, R.J. 1988. Patterns of Allelic Variation in Natural Populations of *Abies fraseri* (Pursh.) Poir. Ph.D. Thesis, North Carolina State University, Raleigh, North Carolina. 119 p.

Rudinsky, J.A. 1956. Notes on the balsam woolly aphid. Presented by Pacific Northwest Forest and Range Experiment Station at annual meeting of Northwest Forest Pest Action Council, 10/29/56 in Portland, Oregon. Weyerhaeuser Timber Company. 12 p.

Saigo, R.H. 1976. Anatomical changes in the secondary phloem of grand fir (*Abies grandis*) induced by the balsam woolly adelgid (*Adelges piceae*). *Canadian Journal of Botany* 54:1903-1910.

Schooley, H.O. 1974. Balsam woolly aphid damage to the crowns of balsam fir trees. Can. For. Serv. Nfld. Inf. Rep. N-X-121. 27 p.

Schooley, H.O. 1976. Recovery of young balsam fir trees damaged by balsam woolly aphid. *For. Chron.* 52:143-4.

Schooley, H.O. and D.G. Bryant. 1978. The balsam woolly aphid in Newfoundland. Canada Forest Service, Newfoundland Forest Research Centre, Inf. Rep. N-X-160. 72 p.

Sidebottom, J. 2004. Christmas Tree Notes: Balsam Woolly Adelgid. North Carolina Cooperative Extension Service CTN-020. 4 p.

Silver, G.T. 1959. The balsam woolly aphid, *Adelges piceae* (Ratz.) in British Columbia. Bi-Mon. Progress Report, Can. Dept. Forest. 15(1):3.

Slama, K. and C.M. Williams. 1965. Juvenile hormone activity for the bug *Pyrrhocoris apterus*. Proc. Natl. Acad. Sci. USA 54:411-414.

Smith, F.H. 1967. Effects of balsam woolly aphid (*Adelges piceae*) infestation on cambial activity in *Abies grandis*. *American Journal of Botany* 54:1215-23.

Speers, C.F. 1958. The balsam woolly aphid in the Southeast. *Journal of Forestry* 56:515-516.

Timell, T.E. 1986. Compression Wood in Gymnosperms. Volume 3. Ecology of compression wood formation, silviculture and compression wood, mechanism of compression wood action, compression wood in the lumber and pulp and paper industries, compression wood induced by the balsam woolly aphid, opposite wood. Springer-Verlag. p. 1339-2150.

Varty, I.W. 1956. *Adelges* insects of silver firs. For. Comm., Edinburgh, Bull. 26. 75 p.