FORUM

BALSAM WOOLLY ADELGID (HOMOPTERA: ADELGIDAE) AND SPRUCE-FIR DECLINE IN THE SOUTHERN APPALACHIANS: ASSESSING PEST RELEVANCE IN A DAMAGED ECOSYSTEM

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ABSTRACT

Research on tree decline has shown that the proportion of sapwood area to heartwood area is an important measure of tree health. Infestation by the balsam woolly adelgid (BWA), *Adelges piceae* (Ratz.), causes the formation of abnormal wood, which is thought to conduct sap poorly. BWA infestation is also associated with lower (more negative) xylem pressure potentials and increased areas of heartwood. We hypothesize that lower pressure potentials (a consequence of abnormal wood production) increase the rate of cavitation (gas-filling) of sapwood tracheids, thereby accelerating heartwood formation. If this hypothesis is correct, adelgid attack causes loss of functional sapwood both directly and indirectly.

There is evidence that the balsam woolly adelgid is an important factor causing the decline of Fraser fir, *Abies fraseri* (Pursh) Poir., in the southern Appalachians. However, adelgid damage is probably interacting with many other environmental factors to cause reductions in per cent sapwood area. Determining the relevance of this pest to tree decline can be accomplished by examining the relationship that exists between adelgid infestation, increment growth, and per cent sapwood area.

Resumen

En investigaciones se ha demostrado que la proporción alburduramen es una medida que se relaciona con la sanitad y vigor de árboles en decadencia. Infestaciones de el adelgido algodonoso del balsamo (BWA), *Adelges piceae* (Ratz.), causan la formación de madera anormal y disminuyen la conducción de la savia. La infestación de BWA también se asocia con presión potencial baja (negativa) del xilema y con el incremento del duramen. Nosotros sostomos la hipótesis de que presiones potenciales bajas (a consecuencia de la producción anormal de madera) incrementan la tasa de cavitation (llenado de gases) de las tracheidas del albur, causando la acentuación de formación del duramen. Si esta hipótesis es correcta, el ataque del adelgido causa una pérdida directa e indirecta del albur.

Hay evidencia de que el adelgido algodonoso del balsamo es un factor importante para el declive de pino Fraser, *Abies fraseri* (Pursh) Parrot, en el sur de los Apalaches. Probablemente el daño del adelgido está interactuando con otros factores del medio ambiente, lo cual causa reducciones en un porcentaje del área de albur. Para determinar la importancia de esta plaga en el declive del árbol, se puede examinar la relación que existe entre las infestaciones de adelgidos, incremento del crecimiento y el porcentaje del area de albur.
There is little doubt that the balsam woolly adelgid (BWA), *Adelges piceae* (Ratz.), qualifies as an important pest of Fraser fir, *Abies fraseri* (Pursh) Poir. Aerial photographs taken in 1960 near Mount Mitchell, N.C. revealed that approximately 200,000 fir trees had already been killed just five years after BWA was detected in this area (Amman & Speers 1965, Amman 1960). By 1966, 90% of all Fraser fir stems over 8 feet tall in the Mt. Mitchell area had been killed by this insect (Witter & Ragenovich 1966). Today in the Black Mountains surrounding Mt. Mitchell, an estimated 49% of standing Fraser fir trees are dead (Dull et al. 1988). Now that BWA has spread throughout the Black Mountains, it is no longer possible to compare the condition of infested trees with the condition of nearby trees which have never been infested. Thus it is difficult to separate the effects of BWA injury from the effects of other environmental factors.

Much research in the southern Appalachians is directed towards assessing the possible role of atmospheric pollutants in causing a growth decline of both Fraser fir and red spruce (*Picea rubra* (Du Roi) Linkl) (Bruck 1984, Zedaker et al. 1987). Although most researchers recognize that BWA is an important component of the decline problem, it is not clear to what degree this insect is continuing to cause decline symptomology. In order to assess the importance of BWA, we must consider how BWA damage to fir trees might be interacting with other environmental factors which have been hypothesized to cause tree decline. This paper reviews some of the factors that might be important to this interaction.

**BACKGROUND AND HISTORY**

BWA is thought to be native to the silver fir forests of central Europe (Pchorn-Walcher & Zwolfer 1988). This insect, in the family Adelgidae, seldom causes serious injury to fir trees (*Abies* sp.) within its native range (Varty 1956, p. 39). It was first discovered in the southern Appalachians in 1955 (Amman 1966). Although BWA attacks other North American fir species (*Abies* sp.), Fraser fir is one of the most susceptible (Mitchell 1966). BWA does not attack spruce.

Fraser fir is thought to represent a glacial remnant from the Pleistocene (Buell 1945, Cain 1944, Witter & Ragenovich 1966). It occurs in six discrete areas of high altitude in the southern Appalachians. Although not important as a timber source, Fraser fir forests are valuable for their recreational use, and also serve as a good source for the Christmas tree industry.

Most tree mortality has occurred in the southern portion of Fraser fir’s range, from the Black Mountains surrounding Mount Mitchell to the Great Smoky Mountains. Fraser fir trees at Mount Rogers, Virginia have suffered considerably less mortality, despite evidence that BWA has been present at this location since at least 1962 (Haneman et al. 1981). Individual trees at Mount Rogers do become heavily infested, just as they do in other areas where Fraser fir grows (personal observation). Therefore the relatively low mortality of trees in infested areas at Mount Rogers is probably not related to the degree with which trees become infested.

The life cycle of the BWA is comprised of the egg, three nymphal instars, and the adult female, which is wingless and parthenogenic. The first nymphal instar is termed a “crawler.” Only this stage is mobile. After it finds a suitable place to feed, it inserts its stylet into the bark and feeds in that particular spot throughout its life. As an adult it measures approximately 0.80 mm in length, and is covered with white strands of wax which make the insect appear “woolly” (Ralph 1952). BWA completes two or three generations per year in North Carolina (Arthur & Hain 1984). The adelgids feed primarily on the main stem of the tree. Trees that do not recover from infestation generally die within two to five years after initial attack (Amman & Speers 1965).
HOST REACTIONS

Adelgid attack causes chemical and structural changes within the bark of susceptible hosts. Balch (1952) has described these changes in detail for balsam fir (Abies balsamea [L.] Mill.). Initially the number and size of bark parenchyma cells increase within the feeding zone (the area surrounding the insect's stylets). Within one year, the feeding zone becomes surrounded by purplish cork cells. The parenchyma cells within this zone then disintegrate, and the area becomes infiltrated with resin.

The bark of a Fraser fir tree is bounded exteriorly by a persistent periderm layer. As a result, the bark of most trees is comprised almost entirely of inner (living) bark (personal observation; also see Chang 1954). However, beneath areas of bark which are heavily infested, a secondary periderm layer is formed at a depth of two or more millimeters. This process leaves behind a superficial layer of dead cells (outer bark) which physically prevents feeding by future generations of adelgids (Balch 1952). Areas of bark which are heavily-infested during one insect generation might support few (if any) insects during the subsequent generation (personal observation).

Although BWA feeds only from the bark of fir trees, infestations on North American firs typically induce the formation of altered xylem tissue which conducts water very poorly (Balch 1952, Mitchell 1967). In cross-section this wood is evidenced by enlarged growth rings which appear to contain a high proportion of latewood. Because of its color, it is termed "rotholz," a German word meaning "red wood." Microscopic examination shows that rotholz is anatomically similar to compression wood (Balch 1952), having thick-walled tracheids which are circular (as opposed to rectangular) in cross-section (Doerksen & Mitchell 1965, Timell 1986). Rotholz forms only in the vicinity of adelgid attack (Balch 1952; Doerksen & Mitchell 1965). Even low populations of BWA are sufficient to cause its occurrence beneath infested bark (Balch 1952, and personal observation). It has not been reported as occurring in any of the European fir species (Balch 1952, p. 74).

MECHANISM OF INJURY

The bulk of available evidence suggests that the primary damage caused by BWA infestation to North American firs results from the production of abnormal wood. Mitchell (1967) injected acid fuchsin dye into the stems of grand and subalpine firs (Abies grandis (Dougl.) Lindl. and Abies lasiocarpa (Hook.) Nutt., respectively) to investigate the effect of BWA infestation on water uptake by the sapwood. Compared with uninfested controls, infested trees absorbed less dye and transported the dye in fewer growth rings. Dye did not move through areas containing rotholz. Dye uptake experiments have also been conducted on infested and uninfested balsam fir with similar results (Balch 1952, p. 63).

Figure 1 shows the relative positions of the various wood types discussed above in a stem section of a Fraser fir Christmas tree which had been lightly infested for three years.

In general, decline symptoms are similar for all species of North American fir that are infested primarily on the main stem. Differences which do exist apparently result from host sensitivity as well as the spatial pattern of BWA colonization (Mitchell 1966). Symptoms shown by grand and subalpine fir include drooping leaders (Mitchell 1966), positive sap pressures in mid-summer, and water-soaked appearance of heartwood (Mitchell 1967). The crown of grand fir usually dies over a period of years, beginning with the lower limbs and proceeding upwards. Amman (1967) observed a similar pattern for Fraser fir growing on Mount Mitchell. In contrast, the crown of subalpine fir usually
begins dying from the top (Mitchell 1966). All of these symptoms are consistent with the hypothesis that BWA induced damage impeded water transport in the sapwood.

For some heavily-infested trees, bark and cambial death apparently precede crown deterioration. This has been observed for balsam fir (Balch 1952) and Fraser fir (personal observation). In these cases, death of the bark and cambial tissues effectively “girdle” the trees. Within a year’s time, the foliage of the entire crown becomes chlorotic, then changes to a russet red color. Balch suspected that this rapid tree death was the direct result of damage to the bark and cambium. To test this hypothesis, he selected four healthy balsam fir trees and, for each tree, removed a band of bark tissue by cutting with a scalpel. The depth of the cut and the width (height) of the band was varied between trees. The tree which received the most bark injury (5-foot-wide band, 3 mm deep) exhibited symptoms identical to those trees which were naturally “girdled” by BWA. Considering the rapid nature of decline symptoms, we believe that disturbance of water transport (not interruption of the phloem) is likely to be the proximal cause of tree death. Some girdled trees live for many years before dying (Zimmermann 1983, p. 121; Noel 1970). Perhaps in the case of fir, drying out of bark and cambial tissues leads to cavitation (gas-filling) of sapwood tracheids, thereby increasing resistance to sap ascent. It is unclear what proportion of Fraser fir succumbing to BWA follow this rapid pattern of decline.

Although rotholz production is a common occurrence in infested trees of North American fir species (including Fraser fir), not all infested trees produce rotholz. However the xylem of infested trees can be altered even when rotholz is not produced. Heavily-infested grand fir trees, grown as exotics in Scotland, were found to contain no rotholz, yet the “sapwood” of these trees (wood adjacent to the cambium) was only one-twentieth as permeable as sapwood sampled from nearby uninfested trees. This adelgid-altered
wood stained the same color as heartwood (Puritch 1971). Follow-up studies determined that the reduced permeability was most likely due to a combination of tracheid pit membrane encrustation and increased volume of air in the sapwood (a consequence of accelerated cavitation, or gas-filling of tracheids) (Puritch & Johnson 1971, Puritch & Petty 1971). A subsequent trial using grand fir from British Columbia found that BWA infestation was associated with an increase in both heartwood area and number of heartwood rings. Within an infested tree, the amount of heartwood was greater adjacent to areas of bark supporting higher BWA populations (Puritch 1977). Based on these results, Puritch and Johnson (1971) advanced the hypothesis that infestation by BWA caused the formation of "premature heartwood."

Pressure chamber measurements on cut shoots of Fraser fir add additional evidence that infestation interferes with water transport through the sapwood. Measurements taken in June showed that infested trees at Mount Mitchell and Roan Mountain, N.C., had lower xylem pressure potentials (an indication of poorer water status) than uninfested controls, while the infested and uninfested trees at Mt. Rogers, Virginia did not differ from one another. In mid-summer, there were no significant differences at any site. In September however, infested trees showed lower water potentials at all locations (Arthur 1985). As September is traditionally a low-rainfall month in the southern Appalachians, these results indicate that the physiological effects of BWA damage are more severe during periods of low rainfall.

In summary, the most important consequence of BWA infestation is a reduction of effective sapwood area leading to increased flow resistance in the sapwood.

Having established the probable mechanism of BWA injury, we can now consider how other environmental factors suspected to cause tree decline might be interacting with effects caused by the Balsam Woolly Adelgid. By so doing we hope to devise a reasonable method for determining the relevance of BWA in the context of a damaged spruce-fir ecosystem. We will use the Black Mountains of North Carolina as a case in point.

**TREE DECLINE**

Approximately 7200 acres of spruce-fir forest are contained within the rugged Black Mountains of North Carolina. The peaks stretch along a single twelve-mile long ridge with a north-south orientation. The percentage of Fraser fir in the stand component increases with elevation, up to 66% at elevations above 6000 feet. Approximately 11% of the spruce-fir type in the Southeast is within this region (Dull et al. 1987, Dull et al. 1988).

Disturbance by humans has been intense in this area (Pyle & Schafale 1988). Most notable is the logging and associated slash fires with subsequent erosion and windthrow problems. The majority of the logging operations occurred between 1912 and 1922, but salvage logging of windthrown trees continued until at least 1929. Other man-made disturbances resulted from grazing, tourism, and fires set by hunters prior to commercial logging.

Within the Black Mountains, both red spruce and Fraser fir are now declining, as evidenced by crown condition, growth increment, and mortality data. The decline has been most severe at the higher elevations, which also contain the highest proportion of fir (Bruck 1984, Bruck & Robarge 1988, Dull et al. 1988, Zedaker et al. 1987). From Mount Mitchell there is evidence that acidic cloud water is responsible for leaching of both calcium and magnesium from the forest canopy (Robarge et al. 1987).

The incidence of Fraser fir mortality is highly correlated with the presence of BWA (Zedaker et al. 1987). However it should be noted that the highest elevations, where fir dominates over spruce, probably receive greater inputs of atmospheric pollutants
due to higher precipitation and frequent cloud immersion (Dull et al. 1987). In this context, Hain and Arthur (1985) hypothesized that atmospheric pollutants may either lower the tolerance of Fraser fir to BWA, or add a final, lethal stress to trees already heavily stressed by BWA.

There is a growing consensus in Europe that pollution-induced deficiencies of soil nutrients are responsible for much of the forest decline observed there (Pitelka & Raynal 1989). Blank et al. (1988) summarized current hypotheses regarding pollutant effects in Europe, and emphasized that no single hypothesis explains all of the observed “decline types.” One common type of decline exhibited by Norway spruce, *Picea abies* L. Karst, at high altitudes in Germany is defined by the yellowing and subsequent loss of older, magnesium-deficient needles. Blank et al. suggested that naturally low levels of magnesium in the soil predispose the spruce to deficiency caused by the leaching action of excess inputs of nitrogen and sulphur. The loss of needles would be expected to reduce the growth potential of the cambium.

Shortle & Smith (1988) hypothesized that calcium deficiency, induced by excess aluminum in the soil solution, is responsible for the red spruce decline in the northeastern United States. They noted that calcium is incorporated at a constant rate in the production of sapwood (regardless of tree vigor), and they used this fact to argue that calcium availability is a limiting factor for cambial growth. Because the demand for calcium per unit of cambial area is constant, the need for calcium (which is not recovered from the heartwood) increases exponentially as the tree grows. Calcium-deficient trees will have reduced sapwood area, leading to crown thinning and susceptibility.

Although the mechanism causing decline differs between these two scenarios, both scenarios result in reduced annual increment, which is evidenced by narrow growth rings. These narrow growth rings are associated with reduced sapwood area. Shortle & Bauch (1986) found this to be the case for declining balsam fir in the U.S. and silver fir (*Abies alba* Mill.) in West Germany. Their results indicated that trees with less than 25% basal area of sapwood become highly vulnerable to death from secondary pathogens and insects. The vulnerability occurs because less sapwood is available for defense, food storage, and water conduction (Shortle & Bauch 1986, Shortle & Smith 1988).

A reduced proportion of sapwood area results from a reduced rate of sapwood production, an accelerated rate heartwood formation. According to Huber, the loss of water from the tracheids is the “beginning of a chain of events which we call heartwood formation” (Zimmermann & Brown 1971, p. 212). Loss of water from the tracheids occurs when the tracheids cavitate. As sapwood ages, the proportion of tracheids which are cavitated gradually increases (Zimmermann 1983, p. 46). This is a least part of the reason why inner sapwood is generally less permeable than outer sapwood (Puritch 1971).

**Interaction of BWA Damage with other Environmental Factors**

As previously discussed, trees infested by BWA contain poorly-conducting sapwood rings and a greater proportion of heartwood. A reduction in effective sapwood area caused by BWA may lead to a lower (more negative) xylem pressure potential in the stem of an infested tree. According to Darcy's Law, the flow rate of a liquid through a porous material is equal to: [cross-sectional conducting area × permeability × pressure difference] ÷ [viscosity × specimen length] (Puritch 1971). For a given rate of sapwood flow, loss of sapwood area should cause pressure differences in the main stem to increase, assuming all other factors are held constant. Thus negative xylem pressures in the stems may become more negative in response to sapwood loss. Trees might compensate for lost sapwood area by dropping foliage or reducing transpiration. However there is experimental evidence (as discussed in the Introduction) that pre-dawn xylem pressure potentials are in fact lower (more negative) in infested versus uninfested trees. This indicates that compensation, if it occurs, is incomplete.
As pressure in the main stem becomes more negative, the relative frequency of cavitation (gas-filling) of sapwood tracheids is expected to increase (see Zimmermann 1983, p. 46). As previously mentioned, the loss of water from sapwood tracheids may initiate the process of heartwood formation (Zimmermann & Brown, 1971, p. 212). Thus we suggest that BWA damage accelerates heartwood formation by increasing the rate of cavitation of sapwood tracheids. If BWA attacks a tree whose cambial growth potential has already been reduced by other environmental factors, then per cent sapwood area may be reduced to the point that the tree succumbs to insects, disease, or drought.

RESEARCH DIRECTIONS

If BWA interacts with other environmental factors to cause an reduction in per cent sapwood area, studying the interaction fully will require knowing the infestation history for each tree. Reasonably accurate infestation histories can be constructed by examining tree rings for the presence of rotholz.

Rotholz can usually be distinguished from true compression wood because the latter is seldom formed on both sides of the tree simultaneously. The presence of rotholz in a tree ring can be determined by examining wood cores collected from opposite sides of a tree. Unfortunately our experience suggests that heartwood-sapwood boundaries cannot be reliably determined from Fraser fir wood cores. Apparently the cores do not provide enough surface area for perceiving the generally slight color differences between sapwood and heartwood which occur when Fraser fir wood is reacted with 40% perchloric acid (following the method of Eades 1988). Assessing heartwood-sapwood boundaries may require cutting down a limited number of sample trees from protected areas. Data on rotholz histories and per cent sapwood areas could be used for testing the hypothesis that BWA infestation accelerates the formation of heartwood. In addition, it could be used to test for an interaction of BWA injury and tree decline (as measured by growth increment data) for Fraser fir growing in the Black Mountains of North Carolina.

REFERENCES CITED


