

Influence of plant-hardiness zone, shoot length, and crown class on the incidence of gouting by the balsam woolly adelgid on balsam fir

Bertrand Guillet, Andrew Morrison, Drew Carleton, Don Ostaff, Dan Quiring

Abstract—We collected midcrown branches of balsam fir, *Abies balsamea* (L.) Mill. (Pinaceae), at six different sites located in five different plant-hardiness zones, along a north–south transect in New Brunswick, Canada, to evaluate the effect of plant-hardiness zone, crown class (overstory *versus* understory), and shoot length during the previous 10 years on the annual incidence of gouting by the balsam woolly adelgid, *Adelges piceae* (Ratzeburg) (Homoptera: Adelgidae). Site, crown class, and their interaction, along with the square of shoot length, explained 78% of the variation in gouting. Variations in gouting attributed to plant-hardiness zone were probably primarily due to variation in mean January temperature: at each site, the mean January temperature was positively and closely related to the mean level of gouting. The level of gouting was consistently higher on trees in the understory than on those in the overstory. Shoot length was parabolically related to the proportion of shoots with gout. The parabolic relationship between shoot size and the level of gouting is similar to that previously reported for galling adelgids, and suggests that gouting by *A. piceae* may be greatest on trees with an intermediate growth rate.

Résumé—Nous avons récolté des branches de sapin baumier, *Abies balsamea* (L.) Mill. (Pinaceae), au niveau du milieu de la cime dans six sites différents situés dans cinq zones distinctes de rusticité végétale suivant un transect nord-sud au Nouveau-Brunswick, Canada, afin d'évaluer les effets de la zone de rusticité végétale, du type de cime (étage dominant vs sous-étage) et de la longueur des pousses durant les 10 dernières années sur l'incidence annuelle de renflements provoqués par le puceron lanigère du sapin, *Adelges piceae* (Ratzeburg) (Homoptera: Adelgidae). Le site, le type de cime et leur interaction, de même que la (longueur des pousses)² expliquent 78% de la variation des renflements. La variation des renflements attribuée aux zones de rusticité végétale est probablement due surtout aux variations de la température moyenne en janvier; la température moyenne de janvier à chacun des sites est en corrélation positive et étroite avec la densité moyenne de renflements. L'incidence des renflements est toujours plus importante sur les arbres du sous-étage que sur ceux de l'étage dominant. Il y a une relation parabolique entre la longueur des pousses et la proportion des pousses porteuses de renflements. La relation parabolique entre la taille des pousses et l'incidence des renflements est semblable à celle signalée antérieurement pour la formation de galles d'adelgides et laisse croire que la formation des renflements par *A. piceae* pourrait être maximale sur les arbres à taux de croissance intermédiaire.

[Traduit par la Rédaction]

Received 14 July 2009. Accepted 14 April 2010.

Bertrand Guillet, Andrew Morrison, Drew Carleton, Dan Quiring,¹ Faculty of Forestry and Environmental Management, University of New Brunswick, Fredericton, New Brunswick, Canada E3B 5A3

Don Ostaff, Faculty of Forestry and Environmental Management, University of New Brunswick, Fredericton, Canada E3B 5A3, and Atlantic Forestry Centre, Canadian Forest Service, Natural Resources Canada, 1350 Regent Street South, Fredericton, New Brunswick, Canada E3B 2G6

¹Corresponding author (e-mail: quiring@unb.ca).
doi: 10.4039/n09-065

Introduction

The balsam woolly adelgid, *Adelges piceae* (Ratzeburg) (Homoptera: Adelgidae), was first introduced into the Maritime Provinces and New England states from Europe approximately 100 years ago (Balch 1934, 1952) and now also occurs in Newfoundland, coastal areas of Quebec, and the west coast of North America (Oregon, Washington, and British Columbia) (Martineau 1984). *Adelges piceae* is a pest of true firs, *Abies* Mill. (Pinaceae); in eastern Canada it is found exclusively on balsam fir, *A. balsamea* (L.) Mill. (Martineau 1984). Juveniles (crawlers) and adults use piercing/sucking mouthparts to feed on host phloem. Balch (1952) reported that a salivary secretion injected into the phloem during feeding causes a swelling or “gout” condition symptomatic of attack by this adelgid. Adults are wingless; this limits dispersal, and infestations build up locally, causing an irregular or spotty distribution of outbreaks (Balch 1952). Severely affected trees are unsuitable for lumber because shrinkage is uneven, causing warping and splitting, and pulp is inferior in quality to that from normal wood (Page 1975; Milne 1990). Average volume losses in highly susceptible semimature and mature stands can be greater than 80% (Page 1975). Stem attack can lead to growth reductions in excess of 50%, with high populations killing trees of merchantable size within 3 years (Balch 1952). Chronic crown infestation can cause a tree to succumb in 10–20 years (Carroll and Bryant 1960). Feeding by *A. piceae* may also predispose balsam fir trees to *Armillaria* root rot (Hudak and Singh 1970).

Previous studies have shown that survival of overwintering nymphs (Greenbank 1970) and the presence of symptoms of *A. piceae* feeding (Quiring *et al.* 2008) in several areas of Atlantic Canada were inversely related to winter temperature. Similarly, the distribution of damage caused by *A. piceae* is closely related to plant-hardiness zone, in large part because of the overwhelming influence of temperature on this insect (Hartling 2004; Quiring *et al.* 2008). Although the influence of low winter temperatures on *A. piceae* survival and the incidence of damage to balsam fir are

well documented, there is little agreement on the influence of other factors on the susceptibility of balsam fir to this adelgid. For example, Page (1975) reported that damage caused by *A. piceae* was greatest at dry sites, whereas Brower (1947) found more damage at poorly drained, wet, shallow sites, and Balch (1934) reported that site quality was not important. Similarly, Schneider-Orelli *et al.* (1929, cited in Balch 1934) and Chrystal (1926) reported that damage caused by *A. piceae* was most prevalent on trees in the sun and shade, respectively, whereas Balch (1934) reported that sun exposure did not influence the amount of damage on host trees.

The wide range of conclusions drawn from previous studies suggests that the parameters measured were either not directly related to damage by *A. piceae* or that their influence was not linear. For example, many site conditions, such as nutrient availability, influence tree growth in a nonlinear fashion (McKinnon *et al.* 1998), and if the survival of juvenile *A. piceae* on balsam fir is parabolically related to tree growth rate or shoot size, as has been shown for galls (including a galling adelgid on spruce (McKinnon *et al.* 1999; Quiring *et al.* 2006)), then relationships between site conditions and the incidence of damage by *A. piceae* may not be straightforward.

As a first step in the development of a hazard-rating system for this pest, we previously showed that the distribution of symptomatic balsam fir trees in Atlantic Canada coincides with areas where the mean January temperature is above -11°C and that are located in plant-hardiness zones warmer than 4a (Quiring *et al.* 2008). Here we report results from a study evaluating the independent effects of site along a plant-hardiness gradient in New Brunswick and shoot length on the incidence of gouting by *A. piceae*. Although *A. piceae* does not form a gall (in which juveniles develop), the mechanism it uses to stimulate the formation of extra tissue in a gouted shoot may be similar to that involved in gall formation. Galling adelgids on spruce, *Picea* A. Dietr. (Pinaceae), reportedly induce gall development by injecting a chemical that enables them to take control of shoot development (Sopow *et al.* 2003). Gall-induction success is apparently dose-dependent:

Table 1. Locations of two balsam fir stands and a nearby weather station at each of six sites along a gradient of plant-hardiness zones in New Brunswick.

Site	Location description	Latitude (°N)	Longitude (°W)	January temp. (°C)*	Plant-hardiness zone
Upsalquitch	Weather station	47.45	-66.41	-12.9 ± 0.4	2b
	Fir stand	47.29	-66.18		3a
	Fir stand	47.41	-66.16		3b
Charlo	Weather station	47.98	-66.33	-11.7 ± 0.4	3b/4a
	Fir stand	47.93	-66.19		3b/4a
	Fir stand	47.92	-66.21		3b/4a
Doaktown	Weather station	46.55	-66.15	-10.7 ± 0.5	4a
	Fir stand	46.61	-65.97		4a
	Fir stand	46.59	-66.07		4a
Fredericton	Weather station	45.92	-66.61	-8.9 ± 0.4	4b
	Fir stand	45.93	-66.66		4b
	Fir stand	45.93	-66.66		4b
St. John	Weather station	45.32	-65.88	-8.19 ± 0.4	5a
	Fir stand	45.33	-65.69		5a
	Fir stand	45.33	-65.78		5a
Point Lepreau	Weather station	45.07	-66.45	-5.1 ± 0.4	5a [†]
	Fir stand	45.18	-66.41		5a [†]
	Fir stand	45.18	-66.44		5a [†]

*Values are given as the mean ± SE.

[†]The Point Lepreau site was located close to the Bay of Fundy and temperatures were considerably lower than at St. John (see the text for details).

a larger dose is required to successfully gall a large bud or shoot (McKinnon *et al.* 1999; Sopow *et al.* 2003; Flaherty and Quiring 2009). Also, because galler success is poor on very small buds/shoots (McKinnon *et al.* 1999; Flaherty and Quiring 2009), presumably because the amount of resources required to make a gall is low (Price 1991), the relationship between the proportion of shoots galled by adelgids and shoot length is often parabolic (Quiring *et al.* 2006). Thus, based on previous work with galling adelgids and with *A. piceae*, we predicted that the proportion of balsam fir shoots with gout would be lowest in cold plant-hardiness zones and would be parabolically related to shoot length.

Methods

Description of study sites and abiotic data

To ensure that stands subjected to a range of climatic conditions were studied, we selected two precommercially thinned balsam fir stands at each of six different sites located in five different plant-hardiness zones in New Brunswick;

all stands were located <15 km from an Environment Canada weather station (Table 1). Plant-hardiness zones were identified using geospatial information provided by Agriculture and Agri-Food Canada at <http://nlwis-snitel.agr.gc.ca/plant00/index.phtml#>. Because of large variations in topography, the weather station and the two nearby stands at the most northerly site were situated in three different plant-hardiness zones. The two stands at Charlo were located along the border between plant-hardiness zones 3b and 4a and were exposed to lower temperatures than were stands at Doaktown, which was situated in the center of plant-hardiness zone 4a. Similarly, although the St. John and Point Lepreau sites are both in plant-hardiness zone 5a, temperatures at the Point Lepreau site were considerably higher, presumably because of its location near the coast. Thus, the six sites represent a gradient of plant-hardiness zones, with the most southerly site (Point Lepreau) located in the mildest zone and the coldest site located at the most northerly location (Upsalquitch). Overstory trees were usually 30–50 years old and regenerating

understory trees were usually <2 m high. We obtained estimates of mean January temperatures from the Environment Canada web site at http://climate.weatheroffice.ec.gc.ca/climate_normals/index_e.html.

Gouting by *A. piceae*

Adelges piceae only causes gouting in current-year shoots. Thus, we were able to determine the percentage of shoots gouted by *A. piceae* during each of the previous 10 years by examining the level of gouting on branches ≥ 10 years old. In 2007 we established five plots (30 m apart) along a transect within each stand as described in Quiring *et al.* (2008) and selected the two overstory and two understory trees that were closest to the center of the plot. Two east-facing midcrown branches were removed from each tree and examined for gouting. Gouting incidence was evaluated for all 1- to 10-year-old shoots on the main axis and on the south-facing half of each branch. To estimate tree growth rates, the lengths (*i.e.*, internodal distances) of 1- to 10-year-old shoots on the main axis were measured. Gouting by *A. piceae* often reduces shoot length growth (unpublished data). However, there is a high degree of branch (Sprugel *et al.* 1991) and even shoot (Quiring and McKinnon 1999) autonomy in conifers, so when a shoot contained gout, the length of an ungouted shoot of the same age on the main axis of an adjacent branch was measured and used in analyses relating shoot length to the level of gouting, a method used successfully with galling adelgids (McKinnon *et al.* 1999).

We pooled data within stands to obtain the mean proportion of shoots with gout and mean shoot lengths for each of the 10 years to avoid pseudoreplication (Hurlburt 1984). Degrees of freedom were slightly fewer than expected (6 sites \times 2 stands/site \times 2 tree sizes/stand \times 10 years of data = 240 df) because some stands lacked 9- and 10-year-old shoots on which we could distinguish the presence or absence of gout. The influence of site, the square of shoot length (shoot length²), crown class (*i.e.*, understory *versus* overstory tree), and the interaction between site and crown class on the proportion of shoots that were gouted, subjected to a square root–arcsine

Table 2. Influence of site, shoot length², tree size (understory *versus* overstory), and the interaction of tree size and site on the proportion of 1- to 10-year-old balsam fir shoots with visible gouting caused by *Adelges piceae* in New Brunswick.

Source	df	Mean square	<i>F</i>	<i>P</i>
Tree size	1	4.119	313.963	<0.0001
Site	5	4.196	63.956	<0.0001
Shoot length ²	1	0.084	6.433	0.0119
Tree size \times site	5	1.161	17.696	<0.0001
Error	213	0.013		
Total	229			

Note: The proportion of shoots with gout was subjected to angular transformation before analysis.

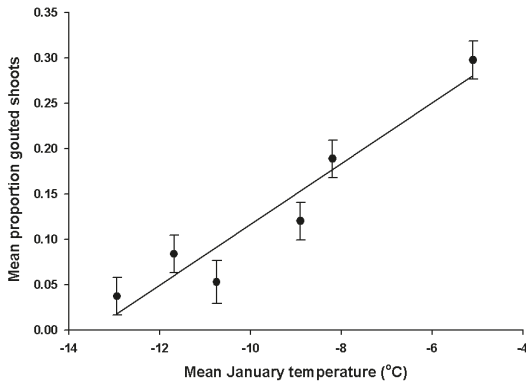
transformation (Sokal and Rohlf 1982), were evaluated using a general linear model. Shoot length² was included in the model to test for a parabolic relationship between shoot length and the level of gouting, as used previously for a galling adelgid (Flaherty and Quiring 2009). When included in preliminary analyses, shoot length (unsquared) was not significant. Regression analysis was used to further examine the influence of independent variables on the proportion of shoots that contained gout. Regression analysis was also used to evaluate the relationships between the proportion of shoots with gout in branches of understory *versus* overstory trees and between the mean January temperature at each site and the mean proportion of gouted shoots.

Results

Site, shoot length², and crown class (overstory or understory) explained 78% of the variation in the proportion of shoots gouted by *A. piceae* during the past 10 years in New Brunswick (Table 2). Because it is the major factor differentiating plant-hardiness zones, temperature is probably the primary factor contributing to the significance of site. A very strong relationship between the mean January temperature at each site and the mean proportion of shoots that were gouted during the past 10 years (Fig. 1) supports this hypothesis.

The mean proportion of shoots with gout was consistently higher in the understory than

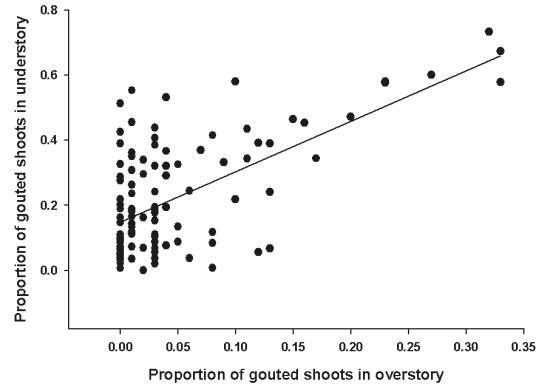
Fig. 1. Positive linear relationship between January temperature (mean \pm SE) in each of six sites in five plant-hardiness zones in New Brunswick from 1997 to 2006 and the mean proportion of balsam fir shoots gouted by *Adelges piceae* during that period (regression equation for means: $Y=0.0335335X+0.4516329$; $R^2=0.92$, $F_{1,4}=44.81$, $P=0.0026$).



in the overstory at all sites across a range of gouting levels (Fig. 2). Variation in the relative differences between levels of gouting in the understory and overstory among sites caused a significant site \times crown class interaction (Table 2). For example, although the proportion of gouted shoots was more than 10 times higher in the understory than in the overstory in St. John (plant-hardiness zone 5a), it was less than twice as high in the understory as in the overstory in Upsalquitch (plant-hardiness zone 3a/3b).

The significant influence of shoot length² on gouting implies that the level of gouting by *A. piceae* is highest on intermediate-sized shoots. To further examine this relationship, we plotted the mean proportion of shoots with gout against shoot length, categorized into 1 cm lengths (Fig. 3). As predicted, the level of gouting was parabolically related to shoot length, being highest on shoots approximately 8 cm in length. There was much variability in this relationship: only 8% of the variation in level of gouting was explained by shoot length when the analysis was carried out with raw rather than pooled data (Fig. 3). This is probably primarily due to the predominant effect of temperature, especially in colder plant-hardiness zones.

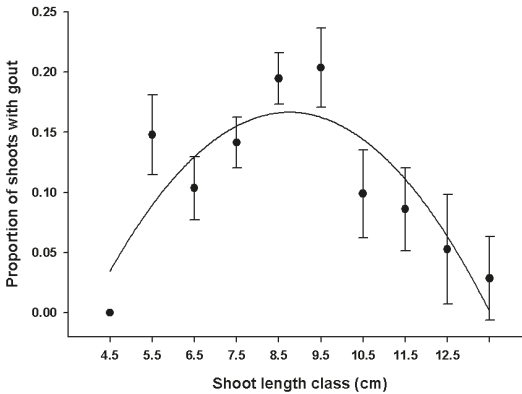
Fig. 2. Positive linear relationship between the proportion of balsam fir shoots gouted by *Adelges piceae* in overstory and understory trees in New Brunswick ($Y=0.1483359X+1.5508079$; $R^2=0.40$, $F_{1,109}=72.61$, $P<0.0001$).



Discussion

Site, tree crown class, and their interaction, along with shoot length², explained most of the variation in the level of gouting during 10 years in stands located along a plant-hardiness gradient in New Brunswick. The strong relationship between the mean level of gouting at each site and the mean January temperature strongly supports the hypothesis that the influence of site is attributable to variation in winter temperature. Previous studies reported that the plant-hardiness zone and the mean January temperature influenced the presence or absence of visible damage caused by *A. piceae* to balsam fir trees (Quiring *et al.* 2008) and that the winter temperature influenced the survival of overwintering fundatrices (Greenbank 1970). Although it was not measured in the present study, the size of gouted nodules appeared to be related to the plant-hardiness zone. Gouted nodules on shoots in the coldest plant-hardiness zones were very small compared with gouted nodules observed on shoots farther south. Similarly, trees in cold, northern sites with low levels of gouting in their crowns did not show obvious symptoms of attack by *A. piceae* when examined visually from the ground, which supports the observations made in previous studies (Quiring *et al.* 2008).

Fig. 3. Relationship between shoot length and proportion (mean \pm SE) of balsam fir shoots in different length classes with gout caused by *Adelges piceae* in New Brunswick (regression equation for means: $Y=0.2127271-0.0056139X-0.0069898X^2$; $R^2=0.61$, $F_{2,7}=5.49$, $P=0.0369$). The regression carried out with raw data was also significant: $Y=0.2022677-0.0050551X-0.0062458X^2$; $R^2=0.08$, $F_{2,227}=9.7039$, $P<0.0001$.



Consistently higher levels of gouting in the understory than in the overstory may have been due to higher winter temperatures experienced by overwintering fundatrices that were covered by snow. Higher levels of gouting on understory trees may also result from higher densities of nymphs, many of which disperse passively in the wind, a behaviour that would result in many of them falling onto understory trees.

The parabolic relationship between shoot length and the mean proportion of gouted shoots supports the hypothesis that the mechanism that results in gouting in balsam fir by *A. piceae* is similar to that which results in galling in spruce by *Adelges abietis* (L.) (McKinnon *et al.* 1999; Sopow *et al.* 2003; Flaherty and Quiring 2009). The parabolic relationship was predicted by the optimal module size hypothesis (Björkman 1998; McKinnon *et al.* 1999) and is based on the assumption that fundatrices inject a chemical stimulus into the vascular tissue that induces gall formation, or in balsam fir, induces gouting. The efficacy of the induction stimulus of adelgid gallers appears to be dose-dependent: increases (Flaherty and Quiring 2009) or decreases (Sopow *et al.* 2003) in the stimulus increase or decrease gall-induction success, respectively. According to this hypo-

thesis, some gallers cannot inject a sufficiently large dose of gall-induction stimulus to take over bud/shoot development and successfully induce a gall. From our study we cannot determine whether or not gouting by *A. piceae* is an intermediary step in the formation of a gall, or whether gouting involves a similar process to gall induction. However, the similar parabolic relationships between shoot length and the proportion of shoots gouted by *A. piceae* recorded by us, and the proportion of shoots galled by *A. abietis* (McKinnon *et al.* 1998), suggest that this may be the case.

Our results strongly suggest that plant-hardiness zone should be included in any hazard rating for *A. piceae*. Furthermore, the contradictory conclusions in previous reports concerning the effects of various site factors may be due to their indirect influence on tree growth rate, and to a potentially parabolic relationship between tree growth, as reflected in the differences in shoot length, and the incidence of gouting by *A. piceae*.

Acknowledgements

We thank Laura Buckingham, Robert Gray, Lindsey Moore, and Amanda Savoie for technical assistance, Ian DeMerchant for spatial referencing assistance, Dan Lavigne, Nelson Carter, Lester Hartley, Lucie Royer, and Hubert Crummey for helpful discussion, Tim Craig for comments on an earlier version of the manuscript, and Forest Protection Limited, SERG International, the Department of Natural Resources of Newfoundland and Labrador, Abitibi-Consolidated, Corner Brook Pulp and Paper, the Natural Sciences and Engineering Research Council of Canada, and Growing Forward for funding. The Canadian Forest Service and the University of New Brunswick provided additional logistical support.

References

- Balch, R.E. 1934. The balsam woolly aphid, *Adelges piceae* (Ratz.) in Canada. *Scientific Agriculture*, **14**: 374–383.
- Balch, R.E. 1952. Studies on the balsam woolly aphid, *Adelges piceae* (Ratz.) (Homoptera: Phylloxeridae) and its effects on balsam fir, *Abies balsamea* (L.) Mill. Canadian Department of Agriculture Publication No. 867.

- Brower, A.E. 1947. The balsam woolly aphid in Maine. *Journal of Economic Entomology*, **40**: 689–694.
- Björkman, C. 1998. Opposite, linear and nonlinear effects of plant stress on a galling aphid. *Scandinavian Journal of Forest Research*, **13**: 177–183. doi:10.1080/02827589809382974.
- Carroll, W.J., and Bryant, D.G. 1960. A review of the balsam woolly aphid in Newfoundland. *Forestry Chronicle*, **36**: 279–293.
- Chrystal, R.N. 1926. The genus *Dreyfusia* in Britain and its relation to the silver fir. *Philosophical Transactions of the Royal Society B Biological Sciences*, **214**: 29–61. doi:10.1098/rstb.1926.0002.
- Flaherty, L., and Quiring, D. 2009. Plant module size and dose of gall induction stimulus influence gall induction and subsequent galler performance. *Oikos*, **117**: 1601–1608.
- Greenbank, D.O. 1970. Climate and the ecology of the balsam woolly aphid. *The Canadian Entomologist*, **102**: 546–578. doi:10.4039/Ent102546-5.
- Hartling, L.K. 2004. A qualitative assessment of the distribution of balsam woolly adelgid on balsam fir in New Brunswick, as detected in 2004. *Forest Pest Management*, New Brunswick Department of Natural Resources, Fredericton, New Brunswick.
- Hudak, J., and Singh, P. 1970. Incidence of *Armillaria* root rot in balsam fir infested by balsam woolly aphid. *Canadian Plant Discovery Survey*, **50**: 99–101.
- Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs*, **54**: 187–211. doi:10.2307/1942661.
- Martineau, R. 1984. *Insects harmful to forest trees*. Minister of Supply and Services Canada, Ottawa, Ontario.
- McKinnon, M.L., Quiring, D.T., and Bauce, E. 1998. Influence of resource availability on growth and foliar chemistry within and among young white spruce trees. *EcoScience*, **5**: 295–305.
- McKinnon, M.L., Quiring, D.T., and Bauce, E. 1999. Influence of tree growth rate, shoot size and foliar chemistry on the abundance and performance of a galling adelgid. *Functional Ecology*, **13**: 859–867. doi:10.1046/j.1365-2435.1999.00376.x.
- Milne, G.R. 1990. An economic analysis of the treatment of balsam woolly adelgid in Newfoundland. Information Report N-X-277, Forestry Canada, Newfoundland and Labrador Region, St. John's, Newfoundland.
- Page, G. 1975. The impact of balsam woolly aphid damage on balsam fir stands in Newfoundland. *Canadian Journal of Forest Research*, **5**: 195–209.
- Price, P.W. 1991. The plant vigor hypothesis and herbivore attack. *Oikos*, **62**: 244–251. doi:10.2307/3545270.
- Quiring, D.T., and McKinnon, M.L. 1999. Why does early-season herbivory affect subsequent budburst? *Ecology*, **80**: 1724–1735. doi:10.1890/0012-9658(1999)080[1724:WDESHA]2.0.CO;2.
- Quiring, D., Flaherty, L., Johns, R., and Morrison, A. 2006. Variable effects of plant module size on abundance and performance of galling insects. *In Gallling arthropods and their associates: ecology and evolution*. Edited by K. Ozaki, J. Yukawa, T. Ohgushi, and P.W. Price. Springer-Verlag, Sapporo, Japan. pp. 189–198.
- Quiring, D., Ostaff, D., Hartling, L., Lavigne, D., Moore, K., and DeMerchant, I. 2008. Temperature and plant hardiness zone influence distribution of balsam woolly adelgid damage in Atlantic Canada. *Forestry Chronicle*, **84**: 558–562.
- Schneider-Orelli, O., Schaeffer, C., and Wiesmann, R. 1929. Untersuchungen über die Weisstannenlaus *Dreyfusia nusslini* C.B. in der Schweiz. *Mitteilungen der schweizerischen Centralanstalt für das forstliche Versuchswesen*, **15**: 191–242.
- Sokal, R.R., and Rolf, F.J. 1982. *Biometry: the principles and practice of statistics in biological research*. 3rd ed. W.H. Freeman and Company, New York.
- Sopow, S.L., Shorthouse, J.D., Strong, W., and Quiring, D.T. 2003. Evidence for long-distance, chemical gall induction by an insect. *Ecology Letters*, **6**: 102–105. doi:10.1046/j.1461-0248.2003.00410.x.
- Sprugel, D.G., Hinckley, T.M., and Schaap, W. 1991. The theory and practice of branch autonomy. *Annual Review of Ecology and Systematics*, **22**: 309–334. doi:10.1146/annurev.es.22.110191.001521.