# The impact of stem galls induced by *Hemadas nubilipennis* Ashmead on shoot characteristics of lowbush blueberry[1]

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Hayman, D. I., MacKenzie, K. E. and Reekie, E. G. 2003. **The impact of stem galls induced by *Hemadas nubilipennis* Ashmead on shoot characteristics of lowbush blueberry.** Can. J. Plant Sci. **83**: 401–408. The effect of galls induced by *Hemadas nubilipennis* Ashmead (Hymenoptera: Pteromalidae) on the morphology and reproduction of lowbush blueberry (*Vaccinium angustifolium* Aiton) was studied over two seasons in three Nova Scotia blueberry fields. Comparisons of galled and non-galled shoot characteristics, and position on shoots of galls formed in the years of vegetative and reproductive growth were made. In June 1999, 30 newly galled vegetative shoots were arbitrarily selected, tagged and measured along with similar sized non-galled shoots on the galled clone and a neighbouring non-galled clone. Shoot characteristics were measured in the reproductive season during bloom and after harvest. At two sites, the dry weights of leaves and stems on galled shoots measured in the reproductive season were significantly less than non-galled shoots, but at a third site there was no difference in stem allocation. Galls reduced berry production on shoots at two sites. Proportions of terminally positioned galls differed significantly among study sites in the reproductive season. Shoots with terminal galls were significantly shorter, lighter and allocated less weight to leaves and stems than shoots with basally positioned galls. If the reports of increasing gall populations in Nova Scotia during the 1990s are correct, there may be good reason to believe that there will be significant economic loss of blueberries in the future.

**Key words**: Gall, blueberry (lowbush), *Hemadas nubilipennis, Vaccinium angustifolium*

Hayman, D. I., MacKenzie, K. E. et Reekie, E. G. 2003. **Incidence des galles de *Hemadas nubilipennis* Ashmead sur les caractères agronomiques du bleuet nain.** Can. J. Plant Sci. **83**: 401–408. Les auteurs ont étudié les répercussions des galles induites par *Hemada nubilipennis* Ashmead (Hyménoptères : ptéromalidés) sur la morphologie et la reproduction du bleuet nain (*Vaccinium angustifolium* Aiton) dans trois bleuetières de la Nouvelle-Écosse, deux saisons durant. Ils ont pour cela comparé les caractéristiques des pousses avec et sans galles et l'emplacement de ces dernières sur la tige pendant les périodes de croissance végétative et reproductive. En juin 1999, ils ont arbitrairement sélectionnés 30 nouvelles pousses portant des galles, les ont étiquetées et les ont comparées à des pousses saines de même taille, les premières ayant été obtenues par clonage d'un plant malade et les secondes par clonage d'un plant sain voisin. Les caractéristiques des pousses ont été déterminées pendant la floraison et après la récolte, la saison de la reproduction. Les feuilles et la tige des pousses portant des galles avaient un poids sec sensiblement inférieur à celui des pousses saines à deux endroits, durant la période reproductive, mais au troisième, le poids sec de la tige était le même. Les galles avaient réduit la production de fruits sur les pousses atteintes aux deux endroits. La proportion de gales en position terminale diffère sensiblement selon le site pendant la période reproductive. Les plants présentant une gale terminale étaient sensiblement plus petits et moins lourds, tandis que leurs feuilles et leurs tiges étaient proportionnellement moins pesantes que celles des plants à galles basales. Si les observations indiquant la prolifération des galles faites dans les années 90 en Nouvelle-Écosse s'avèrent exactes, il y a tout lieu de croire qu'on assistera à une baisse notable du rendement des bleuetières dans l'avenir.

**Mots clés**: Galle, bleuet (nain), *Hemadas nubilipennis, Vaccinium angustifolium*

The native North American lowbush blueberry, *Vaccinium angustifolium* Ait. (Ericaceae), is an important commercial crop in Maine, Atlantic Canada and Quebec (Vander Kloet 1988; Blatt et al. 1989). This species is found on abandoned agricultural land and areas disturbed by clear-cutting or forest fires (Hall 1959; Yarborough et al. 1986). Commercial fields are developed through the manipulation of these naturally occurring stands (Hall and Ludwig 1961). Blueberry grows in clones (genets) that spread by the underground extension of rhizomes (McIssac 1997; Vander Kloet 1988) and there are two seasonal flushes of growth; mid to late spring and early summer (Eck 1988). Developing from dormant buds on rhizomes, new adventitious shoots grow until mid-summer (Vander Kloet 1985). Flower buds are produced in leaf axils and vegetative buds lower on the shoot (Hoefs and Shay 1981). Typically, a 2-yr cropping cycle involves a year of vegetative growth followed by a year of reproductive growth. Following the summer harvest, fields are pruned by mowing and/or burning to stimulate new vegetative shoot growth and fruit buds (Blatt et al. 1989). In addition, a small number of vegetative shoots are produced in the reproductive growth year.

*Hemadas nubilipennis* Ashmead (Hymenoptera: Pteromalidae), forms complex, multi-chambered galls on shoots of *V. angustifolium* and the velvetleaf blueberry *V. myrtilloides* Michaux (Goulet and Huber 1993). Soon after emergence (from mid-May to early July), female gall wasps

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deposit eggs in tender vegetative shoots. Usually after oviposition, an adult female will move up the shoot and cause damage to the apical meristem by repeatedly inserting her ovipositor without oviposition (Shorthouse et al. 1986). When the meristem is killed, a gall will form at the end of the shoot. However, very often the shoot continues to grow resulting in galls forming on the stem. Occasionally in the reproductive year, female wasps will lay on the lateral branches of second year shoots. Eggs hatch in 10–14 d and gall growth and maturation takes a further 60–90 d. If vegetative buds are present below and above the gall, branching occurs. By mid-August the gall is mature, and the enclosed larvae over-winter in diapause within it (West and Shorthouse 1989). Since insect-induced plant galls are physiological sinks that redirect shoot nutrients towards the gall tissue and larvae, it is likely that blueberry stem gall wasp alters resource allocation within its host plant similar to galls of *Phanacis taraxaci* Ashmead in the dandelion (Bagatto et al. 1996). When a female *H. nubilipennis* damages a shoot apex and limits its ability to grow, the gall replaces the apex as the main sink for nutrients and photosynthesis (Shorthouse et al. 1986).

Blueberry producers previously paid little attention to blueberry stem gall populations since they were thought to cause no economic loss. However, stem gall populations were increasing during the 1990s in Nova Scotia (K.E. MacKenzie, unpublished data) and we speculated that galls might reduce berry size and the number of berries. In addition, some galls that are similar in size and shape to berries have been found contaminating both fresh and processed product. There are no known means to manage this insect (Crozier 1997), although the use of burning as a pruning method is thought to provide some measure of control (McAlister and Anderson 1932; Crozier 1997).

A study examining plant physiological response to galls of *H. nubilipennis* during the reproductive season failed to detect differences between galled and non-galled shoots (Galway 1999). However, that study made no distinction between the effects of galls that form at different shoot positions, or in the influence of the pruning regime. We reasoned that these factors could modify plant response to the presence of galls, and ultimately influence crop yield. Our objectives in this study were to: (1) compare the reproductive and morphological characteristics of galled and non-galled shoots within and between clones over a 2-yr production cycle of lowbush blueberry, (2) determine whether there are morphological consequences of gall position for galls formed during the vegetative or reproductive season, and (3) discuss potential economic loss of mature berries by high field densities of galls.

## MATERIALS AND METHODS

Three commercial lowbush blueberry fields in Halifax and Cumberland Counties, Nova Scotia, that fruit in even years were used for the study. Site characteristics are described in Table 1.

### Temperature and Rainfall Records

Monthly rainfall and monthly mean temperatures were obtained for Climate Stations at Jackson (45°35′00″N, 63°51′00″W) and Middle Musquodoboit (45°02′35″N, 63°09′06″W) in Nova Scotia from the Atlantic Climate Centre in Fredericton, NB (Table 2). The Climate Station in Jackson is approximately 7 km ENE of Farmington, while the Middle Musquodoboit Station lays approximately 8 km and 25 km WSW of Greenfield and Dean, respectively. Greenfield, Dean and the Middle Musquodoboit Climate Station are located in the Musquodoboit Valley in the northeastern portion of mainland Nova Scotia approximately 150 km away from the Jackson Climate Station and Farmington site in northwestern mainland Nova Scotia. In Nova Scotia, rainfall events can vary considerably even over short distances (<10 km) and, thus, variation in monthly precipitation is often seen. However, the two growing areas in this study are far enough apart that the use of the two regional Climatic Stations to assess overall precipitation is acceptable (Rob Gordon, personal communication).

### Experimental Design and Measurements

*Vegetative Year (1999)*

At the three sites, 30 individual vegetative blueberry shoots with a newly formed gall in early growth phase (all formed on primary shoots) were arbitrarily chosen on separate clones between 21 June and 5 July 1999. Each of the clones selected had only one newly formed gall on it. An identification number was written on a tag and attached to the lower portion of each galled shoot. Morphological characteristics measured included basal diameter, maximum length in centimetres, and total number of leaves and branches on the shoots. Shoot diameters were measured 5 cm above the ground using a digital caliper (Mitutoya, No. CD-6"CS, Japan). A non-galled shoot on the same clone, and one on a nearby clone without detectable gall infestation but with similar morphological characteristics to the galled shoot were then selected and tagged. Each set of three shoots (galled and non-galled on one clone, non-galled on a neighbouring clone) constituted one block. There were 30 such blocks per site (30 reps × 3 treatments × 3 locations).

*Reproductive Year (2000)*

The numbers of flowers and flower buds were counted for the tagged shoots during bloom on 1 June 2000 in Farmington, and on 2 June 2000 in Dean and Greenfield. Not all of the shoots tagged in 1999 survived the winter or could be found. To determine if shoot morphology and gall position on a shoot was influenced by the season of gall formation (vegetative or reproductive), 30 additional newly induced galls were arbitrarily chosen at each site on clones different from the blocks on 11 July and 14 July 2000 and marked with surveyor flags (30 replications × 3 locations). Of the 90 galls selected, 86 were on first year shoots and four were on second year shoots. Shoot harvest was closely coordinated with the blueberry harvest schedules of the cooperating growers. Harvesting dates were 9, 15 and 18 August 2000 for Farmington, Greenfield and Dean, respectively. Each shoot was clipped at its base at the ground level, placed into a plastic bag and sealed with a twist tie, and then transported back to the laboratory in a cooler. The shoots were stored at 5°C, 45–55% relative humidity until samples were processed (less than 1 wk after clipping).

**Table 1. Site characteristics of study areas used to examine the influence of the blueberry stem gall wasp (*Hemadas nubilipennis* Ashmead) on shoot characteristics of lowbush blueberry**

| Characteristic | Dean | Farmington | Greenfield |
|---|---|---|---|
| Geographical location | 45°11′N, 062°52′W | 45°34′N, 063°54′W | 45°08′N, 063°02′W |
| Field size (ha) | 100 | 18.6 | 15 |
| Years in production | 40 | 40-50 | 17 |
| Productivity | Average | Poor | Good |
| Prune method | Mowed (1996)<br>Mowed and burned (fall 1998) | Always mowed | Mowed (1996)<br>Mowed and burned (fall 1998) |

**Table 2. Monthly rainfall (mm) and monthly mean temperatures (°C) for Jackson and Middle Musquodoboit, Nova Scotia for May–August 1999 and 2000**

| | Monthly mean temperature (°C) | | | | Total monthly rainfall (mm) | | | |
|---|---|---|---|---|---|---|---|---|
| | Jackson[a] | | Middle Musquodoboit | | Jackson | | Middle Musquodoboit | |
| Month | 1999 | 2000 | 1999 | 2000 | 1999 | 2000 | 1999 | 2000 |
| May | 12.7 | 7.8 | 12.7 | 9.0 | 37.2 | 135.8 | 60.4 | 91.0 |
| June | 17.5 | 14.3 | 16.7 | 15.0 | 46.0 | 58.0 | 49.6 | 71.3 |
| July | 19.7 | 17.5 | 19.9 | 17.7 | 46.6 | 105.2 | 66.9 | 83.0 |
| August | 17.4 | 17.5 | 18.6 | 18.3 | 141.6 | 65.8 | 132.7 | 90.4 |

[a]The Jackson Climate Station is approximately 7 km ENE of Farmington. The Middle Musquodoboit Climate Station is approximately 8 km and 25 km WSW of Greenfield and Dean, respectively.

Upon removing a shoot from storage, all individual berries were harvested, counted and classified according to stage of development (immature or mature), then collectively weighed to determine the total fresh berry weight (g). In this study, fruits were classified as mature by the appearance of a light to dark blue colour over the entire surface of the blueberry. The fresh weights of individual mature berries were measured and added together to determine total mature berry weight. Also measured were the number of leaves, maximum shoot length (cm), total shoot leaf area ($cm^2$), total shoot dry weight (g) and total dry weight of the leaves (g). Total shoot leaf area was measured using a leaf area meter (LI-COR model LI-3000, Lincoln, NE). The stem and leaves for each shoot were placed in separate labelled brown paper bags, oven dried for 48 h at 75°C and then weighed directly upon removal from the oven. Ratios for leaf, stem and gall weight were calculated by dividing the weight of these variables by the weight of the entire shoot. For galled shoots, the position of the gall on the shoot (basal or terminal) was determined. Basal galls were located at any point on a shoot below the terminal position, while terminal galls were located at the shoot apex. The dry weight of the gall was measured separately, then together with the rest of the dried shoot.

## Data Analyses

To address the hypothesis that galls alter shoot morphology, raw data for each block were log10 (variate +1) transformed to satisfy the assumption of normality and homogeneity of variance. We then calculated the differences between shoot measurements on galled and non-galled shoots from the same clone, the differences between shoot measurements on galled shoots and shoots on non-galled clones, and the differences between shoot measurements on non-galled shoots on a galled clone and shoots on non-galled clones. These differences were used as the dependent variables in a series of three one-way ANOVAs with site as the independent variable. For each of the three ANOVAs, a student's t-test was used to determine if the overall mean was significantly different from zero; a significant test indicated that the paired shoots differed in morphology. A significant $F$-test for an ANOVA indicated that sites differed in the effect of treatment upon morphology.

Since there were some shoots that died or could not be located, the fruit set data contained many zeros. As a result, Friedman's method for randomized blocks was used to analyze reproductive characteristics. The blocks were analyzed separately by site. All combinations of galled and non-galled shoots were then tested in a pair-wise fashion to determine where differences existed. Differences in the proportion of shoots with flowers, immature berries, mature berries, and both immature and mature berries were compared between galled and non-galled shoots on a per site basis using Fisher's Exact Test.

The significance of differences in the proportion of terminally positioned galls among sites was tested separately by season using Fisher's Exact Test. To test the hypothesis that gall position on a shoot influences shoot allocation patterns, raw data were log10 transformed and analyzed using ANOVA (GLM procedure) with the shoot measurements as dependent variables and site, gall age (formed in the vegetative or reproductive season) and gall position as independent variables. Differences among treatments were considered significantly different at $P \leq 0.05$. All analyses were performed using SAS version 6.12 (SAS Institute, Inc. 1996).

# RESULTS

## Morphological Measurements

Morphological differences between galled and non-galled shoots were found at all three sites (Table 3). At

**Table 3. Vegetative characteristics for galled and non-galled shoots on the same clone, and shoots of a non-galled neighbouring clone from three commercial lowbush blueberry sites in Nova Scotia in August 2000**

| | Dean | | | Farmington | | | Greenfield | | |
|---|---|---|---|---|---|---|---|---|---|
| Variate[z] | Gall ($n$ = 20) | Non-gall ($n$ = 18) | Neighbour ($n$ = 17) | Gall ($n$ = 22) | Non-gall ($n$ = 19) | Neighbour ($n$ = 9) | Gall ($n$ = 20) | Non-gall ($n$ = 15) | Neighbour ($n$ = 10) |
| Number of leaves | 41.95*a* | 38.83*a* | 30.56*a* | 11.64*a* | 47.95*b* | 75.22*b* | 26.22*a* | 46.73*b* | 49.80*b* |
| Total leaf area per shoot ($cm^2$) | 24.36*a* | 20.66*a* | 14.74*a* | 8.92*a* | 45.77*b* | 70.04*b* | 19.27*a* | 32.39*b* | 28.98*ab* |
| Leaf weight ratio | 0.22*a* | 0.37*b* | 0.30*ab* | 0.09*a* | 0.41*b* | 0.36*b* | 0.18*a* | 0.39*b* | 0.31*b* |
| Specific leaf area | 108.60*a* | 146.55*a* | 135.54*a* | 79.94*a* | 193.36*b* | 164.36*b* | 129.46*a* | 186.59*a* | 153.82*a* |
| Stem weight ratio | 0.47*a* | 0.63*b* | 0.64*ab* | 0.67*a* | 0.59*b* | 0.64*ab* | 0.42*a* | 0.61*b* | 0.59*b* |
| Total dry weight (g) | 0.45*a* | 0.30*a* | 0.25*a* | 0.21*a* | 0.59*b* | 1.11*c* | 0.29*a* | 0.39*a* | 0.35*a* |
| Maximum shoot length (cm) | 12.32*a* | 12.04*a* | 10.97*a* | 12.48*a* | 17.80*b* | 20.97*c* | 12.32*a* | 14.02*ab* | 13.61*b* |

[z]Raw data were analyzed as a one-way ANOVA using the differences between treatment-specific variables on galled and non-galled shoots as the dependent variable and site as the independent variable.

*a, b* Values followed by a common letter in a row for each site are not significantly different at $P \leq 0.05$. Means were calculated from raw data. Gall weight was not included in the galled treatments for leaf weight ratio, stem weight ratio, shoots dry weight and total dry weight in order to reveal the effect of galling on plant growth.

Farmington, all but one of the comparisons were statistically significant, at Greenfield about half of the comparisons were significant, and at Dean only two significant comparisons were seen.

Galled shoots in Greenfield had fewer leaves than non-galled and neighbouring shoots, a smaller total shoot leaf area than non-galled shoots, and shorter shoots than neighbouring shoots (Table 3). In Farmington, all three sets of shoots differed from one another in maximum shoot length and total dry weight. For these variates, galled shoot values were smallest, non-galled shoots were larger and neighbours were the largest. Numbers of leaves, total shoot leaf areas and specific leaf areas of galled shoots were significantly smaller than non-galled shoots.

The leaf and stem weight ratio on galled shoots was significantly reduced compared with one of the non-galled shoots for each site (Table 3). The leaf weight ratio of galled shoots was significantly smaller than both non-galled shoots in Farmington and Greenfield, and for non-galled shoots in Dean. Differences among treatments were site specific for stem weight ratio. In Dean, the leaf and stem weight ratio of galled shoots was smaller than non-galled shoots, while the stem weight ratio of galled shoots in Farmington was greater than non-galled shoots. The stem weight ratio of galled shoots was smaller than non-galled and neighbouring shoots in Greenfield (Table 3).

## Shoot Reproduction

Among sites, galls produced the greatest reduction of flowers and berries in Farmington, with less reduction in Greenfield, and none in Dean (Table 4). The number of flowers, berries and berry weight did not differ among shoot treatments in Dean. All reproductive characteristics of galled shoots in Farmington, and the numbers of immature and total berries on galled shoots in Greenfield were significantly lower than those on non-galled and neighbouring shoots. In Greenfield, galled shoots produced significantly fewer flowers and mature berries and had a lower total fresh berry weight than neighbouring shoots, while non-galled shoots produced fewer flowers than neighbouring shoots (Table 4). Treatment had no effect on total mature berry weight in Greenfield.

The proportions of shoots with flowers or with berries were similar for all three shoot types in Dean and Greenfield (Table 5). In Farmington, galled shoots had fewer flowers and all types of berries than did shoots without galls, while non-galled and neighbouring shoots had similar proportions of shoots with flowers and with berries.

## Gall Position on a Shoot

The proportions of galls that were terminal did not differ among sites in the vegetative year, but did differ in the reproductive year (Table 6). In the reproductive season, Farmington had the lowest proportion of terminal galls, while Dean had the highest (Table 6). In the reproductive season, new galls rarely formed on vegetative shoots from the previous season. Of the 30 new galls in Dean, no new galls were found on second year shoots, while $0.10 \pm 0.31$ ($n = 30$) and $0.03 \pm 0.18$ ($n = 30$) galls formed on second year shoots in Greenfield and Farmington, respectively. The proportional increase between seasons was 0.75, 0.59 and 0.22 in Dean, Greenfield and Farmington respectively (Table 6).

## Gall Position Influence on Shoot Morphology

Shoots with basally positioned galls had significantly greater shoot and total dry weights, leaf and stem weight ratios, and maximum shoot length, and significantly lower gall weight ratio and percent of shoot dry weight than shoots with terminal galls (Table 7). The number of flowers, immature, mature and total berries per shoot at each site were not influenced by gall position on a shoot ($\chi^2$, $P > 0.05$). The interaction of gall position × site was significant in explaining maximum shoot length ($F = 3.41$, $P = 0.0357$). Shoots with terminal galls were shorter than basally positioned galls at all sites. The interaction of gall-forming season and site was significant in explaining differences in leaf weight ratio ($F = 5.79$, $P = 0.0038$). Leaf weight ratio was greater on shoots with vegetative year formed galls in Dean and

**Table 4. Reproductive characteristics for galled and non-galled shoots on the same clone and shoots of a non-galled neighbouring clone from three commercial lowbush blueberry sites in Nova Scotia in 2000**

| | Dean | | | | Farmington | | | | Greenfield | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Variate[z] | Gall ($n$ = 22) | Non-gall ($n$ = 18) | Neighbour ($n$ = 17) | $P$ | Gall ($n$ = 24) | Non-gall ($n$ =19) | Neighbour ($n$ = 9) | $P$ | Gall ($n$ = 20) | Non-gall ($n$ = 16) | Neighbour ($n$ = 10) | $P$ |
| Number of flowers | 12.60*a* ($n$ = 20) | 10.41*a* ($n$ = 22) | 13.53*a* ($n$ = 19) | 0.6355 | 0.64*a* ($n$ = 25) | 13.10*b* ($n$ = 21) | 18.55*b* ($n$ = 20) | 0.0021 | 5.55*a* ($n$ = 20) | 11.37*a* ($n$ = 19) | 27.93*b* ($n$ = 15) | 0.0017 |
| Number of immature berries | 1.59*a* | 1.11*a* | 1.41*a* | 1.00 | 0.17*a* | 3.53*b* | 3.44*b* | 0.0002 | 0.45*a* | 1.25*b* | 2.5*b* | 0.0058 |
| Number of mature berries | 5.36*a* | 2.78*a* | 3.88*a* | 0.7152 | 0.04*a* | 4.68*b* | 10.89*b* | 0.0004 | 1.55*a* | 2.88*ab* | 5.2*b* | 0.0050 |
| Total number of berries | 6.95*a* | 3.89*a* | 5.29*a* | 0.7650 | 0.21*a* | 8.21*b* | 14.33*b* | 0.0002 | 2.00*a* | 4.12*b* | 8.7*b* | 0.0047 |
| Total fresh berry weight (g) | 2.09*a* | 0.97*a* | 1.37*a* | 0.8011 | 0.02*a* | 1.98*b* | 5.10*b* | 0.0002 | 0.55*a* | 0.88*ab* | 1.93*b* | 0.0041 |
| Total mature berry weight (g) | 2.02*a* | 0.89*a* | 1.25*a* | 0.4122 | 0.02*a* | 1.77*b* | 4.91*b* | 0.0015 | 0.53*a* | 0.76*a* | 1.70*a* | 0.0968 |

[z]Ranked data were analyzed in SAS using Friedman's test. Differences between treatment responses were determined by pair-wise comparisons.
*a*, *b* Values followed by a common letter in a row for each site are not significantly different at $P \leq 0.05$. Means were calculated from raw data.

**Table 5. The proportion of 2-yr-old galled and non-galled shoots on the same clone and shoots of a non-galled neighbouring clone producing flowers or berries from three commercial lowbush blueberry sites in Nova Scotia in 2000**

| | | Proportion of shoots with variate character | | | |
|---|---|---|---|---|---|
| Site | Variate | Gall | Non-gall | Neighbour | Fisher's exact test probability |
| Dean | Flowers | 0.55 ($n$ = 11) | 0.68 ($n$ = 13) | 0.68 ($n$ = 15) | 0.667 |
| | Immature berries | 0.32 ($n$ = 7) | 0.26 ($n$ = 5) | 0.30 ($n$ = 6) | 0.940 |
| | Mature berries | 0.59 ($n$ = 13 ) | 0.55 ($n$ = 11) | 0.45 ($n$ = 9) | 0.732 |
| | Total berries | 0.59 ($n$ = 13) | 0.58 ($n$ = 11) | 0.45 ($n$ = 9) | 0.653 |
| Farmington | Flowers | 0.08 ($n$ = 2) | 0.71 ($n$ = 15) | 0.65 ($n$ = 13) | < 0.001 |
| | Immature berries | 0.04 ($n$ = 1) | 0.55($n$ = 11) | 0.36 ($n$ = 4) | < 0.001 |
| | Mature berries | 0.04 ($n$ = 1) | 0.60 ($n$ = 12) | 0.45 ($n$ = 5) | < 0.001 |
| | Total berries | 0.08 ($n$ = 2) | 0.65 ($n$ = 13) | 0.45 ($n$ = 5) | < 0.001 |
| Greenfield | Flowers | 0.4 ($n$ = 8) | 0.74 ($n$ = 14) | 0.73 ($n$ = 11) | 0.051 |
| | Immature berries | 0.17 ($n$ = 3) | 0.32 ($n$ = 6) | 0.38 ($n$ = 5) | 0.350 |
| | Mature berries | 0.22 ($n$ = 4) | 0.42 ($n$ = 8) | 0.58 ($n$ = 7) | 0.134 |
| | Total berries | 0.22 ($n$ = 4) | 0.47 ($n$ = 9) | 0.58 ($n$ = 7) | 0.122 |

**Table 6. The proportion of blueberry stem galls that were terminal on shoots of lowbush blueberry from three commercial lowbush blueberry sites in Nova Scotia in the vegetative (1999) and reproductive (2000) years of commercial production**

| | Proportion of terminally positioned galls | | | |
|---|---|---|---|---|
| Gall-forming season | Dean | Farmington | Greenfield | Fisher's exact test probability |
| Vegetative year | 0.15 ($n$ = 3) | 0.38 ($n$ = 9) | 0.20 ($n$ = 4) | 0.269 |
| Reproductive year | 0.90 ($n$ = 28) | 0.60 ($n$ = 18) | 0.79 ($n$ = 23) | 0.021 |

Greenfield, while leaf weight ratio was greater on shoots with reproductive year formed galls in Farmington.

## DISCUSSION

### Effect of Galls on Shoot Growth and Reproduction

Herbivory is known to negatively impact reproductive characteristics of plants such as flower losses, lower fruit number and fruit abortion (Sachi et al. 1988). The response of lowbush blueberry to galling by *H. nubilipennis* was site specific, but generally caused a decrease in reproduction. Reduced reproduction is a common plant response to galls (Fay and Hartnett 1991), due to meristem damage that changes source-sink interactions (Watson and Casper 1984).

The leaf and stem weight ratios of galled shoots were significantly less than at least one of the non-galled shoots at each site. On the whole, these shoot measurements were the most sensitive to gall impact. Galway (1999) did not find differences in leaf allocation between galled and non-galled shoots, perhaps because that study was not designed to test a specific level of gall infestation, nor to measure non-galled

**Table 7. The influence of blueberry stem gall position on the morphology of lowbush blueberry shoots from three commercial sites in Nova Scotia in August 2000**

| | Gall position | |
|---|---|---|
| Variate | Basal ($n$ = 69) | Terminal ($n$ = 85) |
| Shoot dry weight (g) | 0.24 | 0.09 |
| Total dry weight (g) | 0.46 | 0.24 |
| Gall % shoot dry weight | 37 | 66 |
| Maximum shoot length (cm) | 14.14 | 6.17 |
| Leaf weight ratio | 0.17 | 0.04 |
| Stem weight ratio | 0.50 | 0.30 |
| Gall weight ratio | 0.33 | 0.63 |

*Note*: Gall position was significantly different for all variables at $P \leq 0.05$. Since most interactions were not significant except for those discussed in the results, gall position means were calculated from raw data and included all sites and both gall-forming seasons.

shoots on a galled or non-galled clone. Since shoots were tagged between 21 June and 5 July 1999, our results may be conservative, as some shoot growth may have already occurred, especially for galls tagged in early July. Gall wasps on *Acacia longifolia* cause leaf abscission and reduce vegetative growth (Dennill 1985). In a similar way, new stem galls may overpower the sink effects of expanding buds and leaves that use early season carbohydrates coming from rhizomes, thus hindering development. Fay and Hartnett (1991) proposed that apical meristem damage due to gall formation could cause biomass normally allocated to new leaf growth to be shunted to the gall, or pre-existing leaves. Such competition for resources among galls, early forming leaves and buds, meristematic tissues, flowers, fruits and roots may have contributed to differences in weight ratios among sites and treatments.

The sink strength of galls may vary with wasp oviposition date and the number of gall-inducing larvae per gall. A wasp that forms a gall on a shoot before leaves and buds expand may trigger a stronger sink for carbohydrates and amino acids that are stored for the winter than young buds and leaves. Such early season gall formation could be possible since wasp phenology studies by Brooks (1993) and Hayman (1998) have recorded a 14–36 d emergence period for *H. nubilipennis* during the spring growth of lowbush blueberry. Although the number of wasp larvae per gall was not determined in this experiment, previous studies have found that the number of wasps range from 1 to 39 per gall (West and Shorthouse 1989).

## Effect of Clones and Sites

Herbivore attack on an establishing clone can diminish life-long host fitness, whereas such an attack would have negligible impact on mature clones (Abrahamson and McCrea 1986). Differences in reproduction between galled and non-galled shoots on the same clone were common at Farmington, rare at Greenfield and non-existent at Dean. Dean and Greenfield are closer in proximity to one another and subject to similar management strategies and climatic conditions compared with Farmington; therefore the reproductive response of blueberry to galling may vary according to growing conditions. The conflicting results between Dean and Greenfield may be more related to the difference in years in production between these sites.

The optimal growth of lowbush blueberry occurs when there is a monthly average of 100 mm of rainfall from May through August (Benoit et al. 1984), which did not occur at both Climate Stations from May to July in 1999. Since precipitation at the Climate Station near Farmington (Jackson) in May 1999 was 23.2 mm less than the station near Dean and Greenfield (Middle Musquodoboit), moisture levels may have been a factor in reduced shoot growth in Farmington compared with Dean and Greenfield. If so, *H. nubilipennis* may have formed galls in Farmington when shoots and leaves were smaller than the other sites, which would explain the reduced shoot leaf area and total dry weight compared with Dean and Greenfield.

Leaf weight ratio was reduced on galled shoots compared with non-galled shoots, suggesting that galled shoots do not influence leaf production of non-galled shoots on the same plant, or represent an energetic cost to the plant when there is one gall per clone. Since leaf area partly determines carbohydrate reserves on a shoot (Aalders et al. 1969), specific leaf area reduction on galled shoots may have contributed to reduced shoot productivity.

The greatest impact of galls on maximum shoot length was seen at the mowed site in Farmington. Barker and Collins (1963) found that seasonal initiation and termination of growth could be delayed up to a month in fire-pruned areas. Therefore, burn pruning in Dean and Greenfield could have delayed growth in the spring, resulting in reduced reproductive season stem lengths compared with Farmington. Farmington had the greatest berry yields and proportion of shoots with flowers and berries. This was unexpected since Black (1963) determined that burn-pruning can produce large yield increases in controlled experiments.

## Variations in Positions of Galls

Our results suggest that gall position on a shoot is strongly influenced by the stage in the management cycle, and that position strongly influences shoot structure. Proportions of terminal galls increased at each site in the reproductive year, with significant differences among sites. Terminal gall formation may increase with the age of shoots on a clone. Almost all galls that were formed in the reproductive year were on vegetative shoots. Since the proportion of terminal galls increased substantially from the vegetative to reproductive year in the burned sites, burning and site-specific conditions that improve productivity may enhance the formation of terminals galls in the reproductive year.

The behaviour of *H. nubilipennis* stabbing a shoot apex is unusual since damage is not caused by the developing gall larvae, but by the adult female (Shorthouse et al. 1986). Frankie and Morgan (1984) found that gall-forming wasps on Oak (*Quercus fusiformis*) test before ovipositing and lay eggs according to the suitability of the host plant. They proposed that differences in gall architecture and position are caused by variation in insect behaviour. *H. nubilipennis* may respond to limitations of fresh shoots in the reproductive year by thoroughly stabbing the apical meristem in order to acquire sufficient plant resources for offspring development, whereas fresh shoot abundance in the vegetative year may permit more stabbing behaviour variability. A basal positioned gall may result when the apical meristem is not completely damaged by wasp stabbing. Or, wasps may oviposit in meristems on lateral branches of second-year shoots. The morphological differences between shoots with basal and terminal galls were significant. Fay and Hartnett (1991) reasoned that herbivory disrupts the sink vascular system source continuum and results in allocation restrictions when the apical meristem is removed.

### Mature Berry Loss From Galls

A conservative estimate of mature berry loss by galls at a high field density from an average yielding field in Nova Scotia was determined to be 3% (Hayman 2001). This level of loss may or may not exceed the cost to control stem gall by burning depending on yield, field conditions and management, and price being paid for the crop. However, we feel that it is important for blueberry producers to establish stem gall monitoring programs, and carry out control measures such as burning when gall levels are high.

## CONCLUSIONS

The effects of blueberry stem gall on shoot morphology and reproduction varied. Galls reduced shoot vigour and also produced effects on other shoots within a galled clone. Stem gall impact on lowbush blueberry was influenced by gall position and site. Present levels of galls in Nova Scotia blueberry fields may cause an economic loss of berries. Full documentation of growing conditions, wasp behaviour and density of natural enemies in the future may improve our understanding about why galls form at more than one position on a shoot. Finally, an examination of the response of an entire genetic individual (clone) to various levels of gall formation may be useful in determining the consequences of predicted increases in gall populations.

## ACKNOWLEDGEMENTS

We thank Dan Ryan of Agriculture and Agri-Food Canada, Kentville, NS, for guidance during statistical design and analysis; Alana Hayman, Stephanie Chaisson, Walter Wojtas and Julia Reekie for field and laboratory assistance; Keith Crowe, Bruce Mowatt and John Bragg for use of field sites; and the Agri-Focus 2000 Technology Development Program of the Nova Scotia Department of Agriculture and Marketing for financial support. We thank Peter Hicklenton and Mike Hardman of Agriculture and Agri-Food Canada, Kentville, for their careful reviews of the manuscript, and Associate Editor, Peter Toivonen and three anonymous reviewers whose comments much improved the manuscript.

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