Relationship Between Foliar Chemistry and Insect Performance: the Forest Tent Caterpillar

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Popular Summary

Forest tent caterpillar (FTC) feeds on several species of deciduous trees (Stehr and Cook 1968). In northeastern North America, quaking aspen is the preferred host of this spring-feeding insect. FTC commonly defoliates several thousands of hectares of aspen stands each year in Québec (Bordeleau 1990), although its secondary hosts seldom are attacked. Between 1979 and 1982, large outbreaks of FTC occurred in both aspen and sugar maple stands of the southern region of Québec (Bauce et al. 1990). These outbreaks coincided with an episode of crown dieback which affected many broadleaf species. The symptoms were particularly apparent in sugar maple, but aspen was completely unaffected. Although herbivory by FTC was not a major factor explaining sugar maple crown dieback in Québec (Bauce et al. 1990), physical and physiological changes in foliage associated with decline (Houston 1981; Klein and Perkins 1988) are likely to affect foliage quality for herbivorous insects. Despite that forest decline and insect outbreaks often coincide and that foliar chemistry of declining trees is likely to change in ways relevant to insect performance, the response of herbivorous insects to these changes seldom has been investigated (but see Landsberg 1990 *a b c*). Here, we present results of a study in which the performance of FTC larvae on aspen, and healthy and declining maples was compared; we also report leaf chemistry and compare insect performance to these data.

Material and Methods

Sampling of Foliage

Foliage of quaking aspen was collected on trees (n=5) in a stand in Ste-Foy, Québec (46°47' N, 71°21' W). The foliage of sugar maple was sampled from trees in a stand in the southern part of Québec (46°10' N, 71°42' W). Condition of sugar maple trees was evaluated following the classification of Bauce and Allen (1991). Trees with less than 15 percent of the foliage missing from the crown were classified as healthy. Those with more than 50 percent missing foliage were classified having severe dieback. Three (1989) and five (1990) maple trees in each of these two classes were randomly selected for insect rearing and chemical analyses. Foliage of both species was collected early in the morning every 2 to 3 days from the top third of the crown. Leaves for chemical analyses were removed immediately from the twigs and placed on ice in a cooler until they were stored at -80 °C. Foliage for insect rearing was left on the twigs and brought in a cooler to the laboratory where it was placed in distilled water.

Constituents of Foliage

Variables measured were water content (1990 only), total micro-Kjeldahl nitrogen (1990 only) (Allen 1974), free soluble sugars (Renaud and Mauffette 1991), total phenolics (Swain and Hillis 1959), and condensed tannins (Govindarajan and Mathew 1965). Free soluble sugars, total phenolics, and condensed tannins were not measured on aspen in 1989.

Insect Rearing

Egg masses of the FTC were provided by G. Bonneau (Ministry of Natural Resources) and were collected during Marsh from one location in 1989 and from two locations in 1990. At both locations, populations of the FTC were established on aspen. Egg masses were kept at 4 °C until rearing started. Rearing started within 3 to 4 days following budburst in the maple stand and was conducted in growth chambers (22 °C, 80 percent relative humidity, and 16 hr photoperiod). Newly hatched larvae from several egg masses were randomly assigned to feed on the foliage of aspen or on healthy or on declining maples until they reached pupation. Individual leaves were offered to the larvae in Petri dishes. A vial of distilled water was glued to the side of the dish and the leaf petiole was inserted in the vial to maintain turgor. Pupal weight and time to pupation were recorded. Because of the gregarious life-style of FTC, five larvae were reared per Petri dish. To avoid pseudoreplication (Hurlbert 1984), performance data used in statistical analyses were mean pupal weight and mean development time per dish. Alpha=0.05 was the nominal indicator of significance.

Results and Discussion

Foliar Chemistry

Water content decreased in foliage of all species as the season advanced, but the rate of decrease was faster in aspen than in either healthy or declining maples (Fig. 1); a test for the homogeneity of slopes had significant foliage by day interaction term (test performed on $\log_{10}$-transformed data to linearize; $F_{2,110} = 4.00$, $p = 0.0210$). The total nitrogen content decreased at the same rate in foliage of all species as the season advanced ($\log_{10}$-transformed data, F-value for the foliage by day interaction term = 2.73, *d.f.* = 2, 63, $p = 0.0730$). The mean nitrogen content was lower in declining maple than in either healthy maple or aspen (Fig. 1; adjusted least-square means, $p < 0.05$). Multivariate analysis of variance (MANOVA) for repeated measures was used to compare soluble sugar (SS) content among the three foliage

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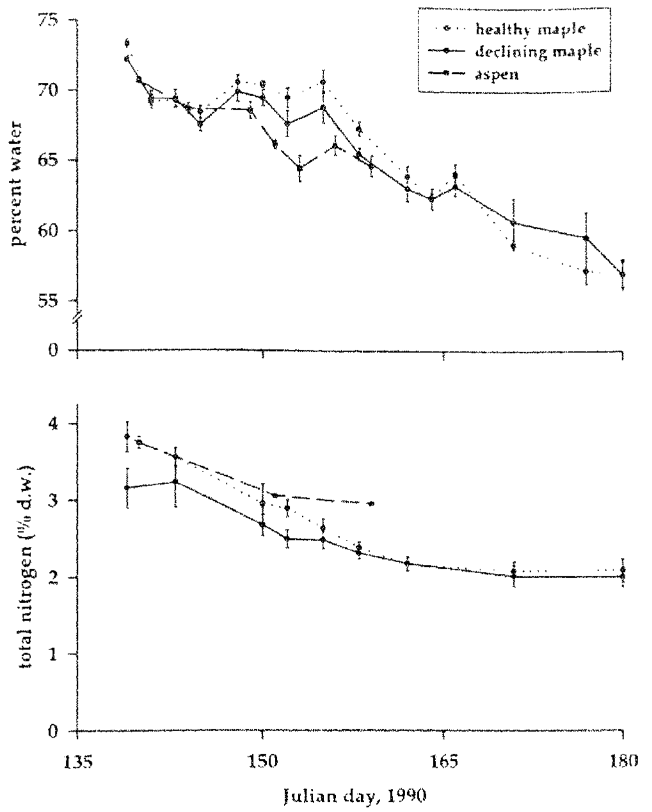

Figure 1.—Water and total nitrogen content of hosts.

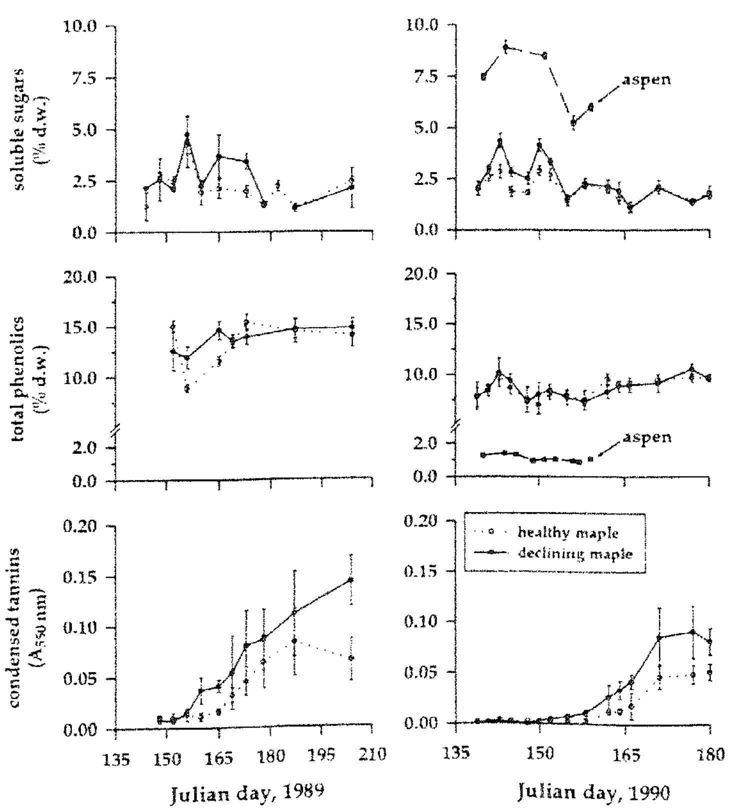

Figure 2.—Total soluble sugar, total phenolic, and condensed tannin content of hosts.

sources. Data included in the analyses were determined by inspecting plots of SS content versus Julian day (Fig. 2). For example, a visual inspection of such plots suggested that the SS content of declining maple foliage was higher than in healthy maple foliage between Julian days 160 and 178 for 1989, and between Julian days 139 and 155 of 1990. Results indicated that there was indeed more SS in the foliage of declining trees for 1990 ($F_{1,7}$ = 15.01, p = 0.0061), whereas no significant difference was found between healthy and declining trees in 1989 ($F_{1,4}$ = 5.76, p = 0.0743). Data for aspen were not included in the analysis because the SS content of aspen foliage was more than twice that in maples (Fig. 2). Interestingly, both species showed the same variation with respect to Julian day, despite the fact that the maple and the aspen stands were separated by 80 kilometers. The mean total phenolics (TP) content in maples was more than 50 percent higher in 1989 (13.5 percent dry weight [d.w.]) than in 1990 (8.6 percent d.w.) (Fig. 2). There was no significant linear trend in either year, as determined by a repeated measures MANOVA (1989: Wilk's Lambda = 0.0027, p = 0.0780; 1990: Wilk's Lambda = 0.0111, p = 0.2127). No significant difference was found between healthy and declining trees (1989: $F_{1,4}$ = 1.10, p = 0.3544; 1990: $F_{1,7}$ = 1.10, p = 0.7898). The TP content was nearly eight times less in aspen than in the maples (Fig. 2). Condensed tannins (CT) started to accumulate in the leaves of maples after Julian day 152 in 1989 and after Julian day 150 in 1990 (Fig. 2), though no significant linear trend was detected by the repeated measures MANOVA (1989: Wilk's Lambda = 0.0342, p = 0.2742; 1990: Wilk's Lambda = 0.7442 , p = 0.0555). This may be due to the large variation among trees, but also to variation between sampling dates within the same tree. Baldwin et al. (1987) reported a similar pattern in their study of leaf tannin variation in sugar maple and yellow birch. In 1990, however, the mean CT content was significantly higher for declining compared to healthy trees ($F_{1,7}$ = 6.33, p = 0.0400). In 1989, the mean CT content tended to be higher in declining trees (Figure 2), but not significantly so ($F_{1,4}$ = 1.93, p = 0.2370). CT were practically absent in aspen (A_{550nm} < 0.008, all dates).

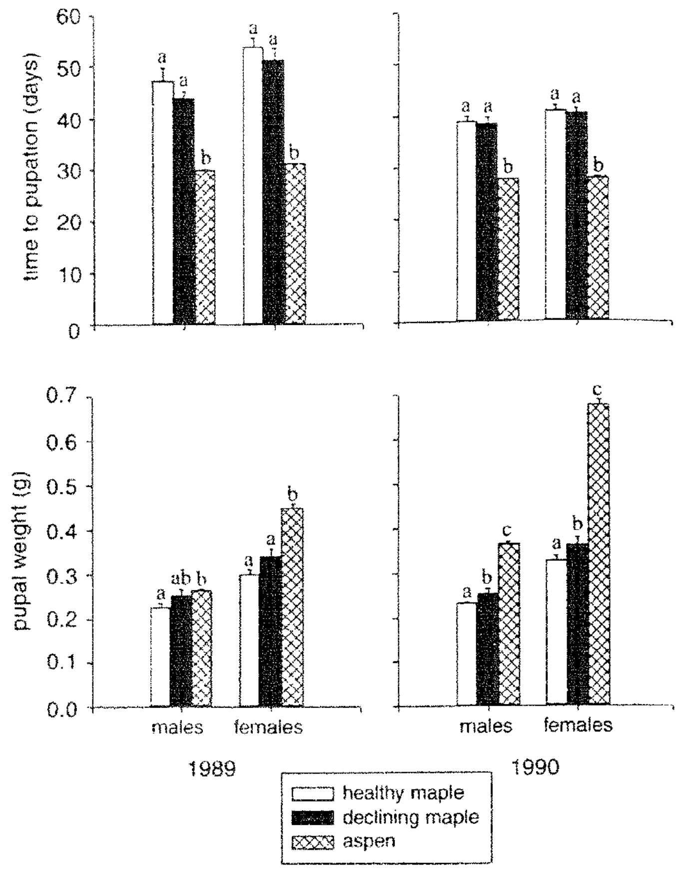

Figure 3.—Time to pupation and pupal weight of Forest Tent Caterpillar on hosts. Different letters above the bars indicate significant differences among hosts within sexes (Waller-Duncan, p = 0.05).

Insect Performance

In both years and in both sexes, FTC larvae developed significantly faster on aspen than on maple (Fig. 3; 1989, males: $F_{2,12}$ = 16.16, p = 0.0004; 1989, females: $F_{2,12}$ = 26.83, p = 0.0001; 1990, males: $F_{2,25}$ = 57.25, p < 0.0001; 1990, females: $F_{2,25}$ = 93.47, p < 0.0001). Development time was not significantly different between healthy and declining maples in either year or in either sex (Fig. 3; Waller-Duncan test at p = 0.05). In 1989, differences in pupal weight were marginally significant in males (Fig. 3; $F_{2,12}$ = 3.72, p = 0.0554), whereas differences were highly significant in females (Fig. 3; $F_{2,12}$ = 23.18, p = 0.0001). In 1990, differences in pupal weight were highly significant in both sexes (Fig. 3; males: $F_{2,25}$ = 100.12, p < 0.0001; females: $F_{2,25}$ = 220.22, p < 0.0001). Both male and female FTC pupae were significantly heavier on declining maple than on healthy maple in 1990 (Fig. 3; Waller-Duncan test at p = 0.05), but not in 1989. FTC pupae were significantly heavier on aspen than on maple, but not in males in 1989 (Fig. 3; Waller-Duncan test at p = 0.05). In both years and in both sexes, ranking of pupal weight was, however, consistent (healthy maple < declining maple < aspen; Fig. 3).

Insect Performance *vs* Leaf Chemistry

High water and nitrogen contents are predicted to increase insect performance (Scriber and Slansky Jr. 1981). Here, variations in water and nitrogen contents among hosts observed in 1990, and the associated response of FTC larvae are inconsistent with this prediction. In aspen, water content was lower than in maples, yet FTC pupae were significantly heavier on aspen than on maples. Declining maple had a lower nitrogen content than healthy maple, yet FTC pupae were heavier on declining maple. Defensive compounds such as soluble phenolics and condensed tannins are generally detrimental to herbivores (Feeny 1968). Here, condensed tannins tended to be higher (1989), or were significantly higher (1990), in declining than in healthy maple, yet FTC pupae were heavier on declining maple. The only consistent relationship between host chemistry and FTC performance that emerges from the results obtained here is between pupal weight and the soluble sugar content of the hosts. In fact, it is possible to correlate pupal weight with the soluble sugar content on a per tree basis, across hosts and across years (Fig. 4). Female pupal weight increased exponentially with increasing soluble sugar content ($y = a\,e^{bx}$; a = 0.239 ± 0.008, b = 0.137 ± 0.006, R^2_{adj} = 0.97, $p < 0.0001$), while the relation was linear for males (y = ax + b; a = 0.025 ± 0.002, b = 0.179 ± 0.007, R^2_{adj} = 0.94, $p < 0.0001$). The exponential relationship for females can be explained by the allometric relationship between pupal weight and the number of eggs at adult emergence (data not shown). When the number of eggs is used, female performance is linearly related to the soluble sugar content of the foliage (Fig. 4; y = ax + b; a = 26.9 ± 2.1, b = 55.8 ± 10.4, R^2_{adj} = 0.93, $p < 0.0001$). Although the very high proportion of the variation in insect performance explained by these models can be due to the gap in the data set at intermediate values of sugar content, it can be seen that the scatter around the predicted values is in general very small (Fig. 4). The results presented here do not necessarily mean that other constituents of leaves have no effect on the performance of the FTC. For example, FTC larvae took longer to develop on maples in 1989 than in 1990 (Fig. 3), and the total phenolics content of maples were higher in 1989 than in 1990, a pattern consistent with the general mode of action of these defensive compounds. The results do, however, indicate the overriding importance of soluble sugars in the diet of the FTC, especially when fecundity is concerned. Only a few other studies have reported increased insect performance with increasing sugar content in the diet (Chippendale and Reddy 1974; Harvey 1974; Valentine et al. 1983).

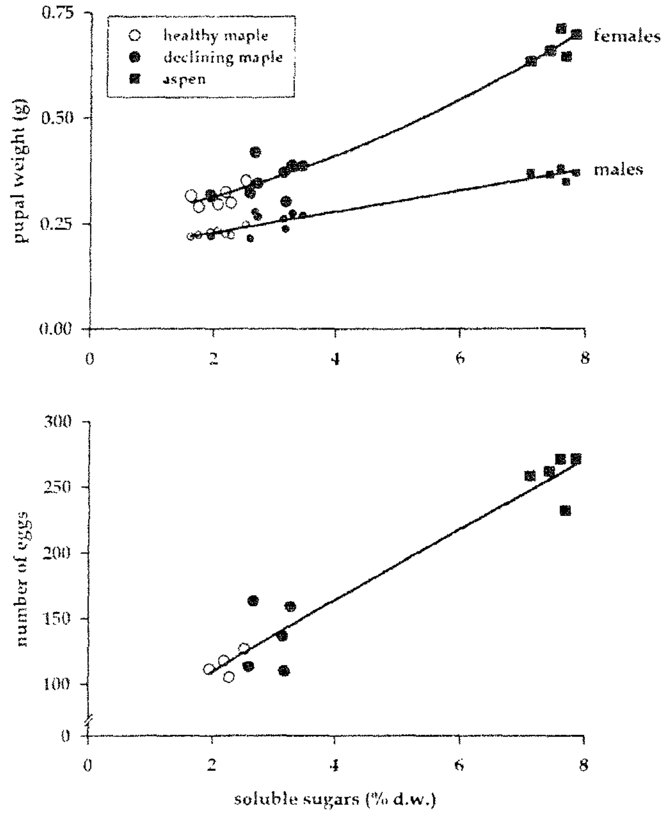

Figure 4.—Mean pupal weight and mean number of eggs per tree in relation to the soluble sugar content of foliage.

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