LEAF QUALITY AND THE HOST PREFERENCES OF GYPSY MOTH IN THE NORTHERN DECIDUOUS FOREST

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ABSTRACT

Both gypsy moth host preferences and the foliage characteristics that have been implicated as factors in host selection were monitored from 1979 to 1982 in a Quercus-Acer-Ostrya forest near Montréal, Québec. The preliminary analyses of these data suggest the hypothesis that gypsy moth larvae preferentially attack trees that have high sugar:tannin ratios in their young foliage.

The gypsy moth, Lymantria dispar L., is recognized as unusually polyphagous both in its native Eurasian habitats and also in eastern North America where it is introduced. Of the approximately 185 trees native to Europe (Polunin and Everard 1976) gypsy moth larvae have been reported to feed on the foliage of 75 (Kurir 1952; Györfi 1960). Similarly in the forests of northeastern North America where the gypsy moth has become established, the larvae can feed on at least 86 (Mosher 1915; Forbush and Fernald 1896) of the approximately 169 available native trees (Little 1979). Such a high degree of polyphagy among tree-feeding macrolepidopterans is matched by only a very few species (Fig. 1). This potential breadth of diet combined with the fact that not all trees are equally preferred as hosts (Lechowicz and Jobin 1983) makes the gypsy moth especially useful in developing and testing hypotheses about the interactions between woody plants and the herbivores that feed on their leaves. The gypsy moth essentially provides a bioassay to call attention to traits that make trees better or worse hosts to defoliating insects. If we can understand the basis for gypsy moth host selection, we may hope to gain some general insights into the forest defoliator-host interaction, particularly into the causes and potential control of insect outbreaks leading to catastrophic defoliation.

Two general types of explanation have been put forward as mechanisms underlying host selection by lepidopteran larvae. These may be distinguished as behavioral versus ecological explanations. Behavioral explanations focus attention on proximate cues involving repellent and attractant compounds that influence larval feeding behavior; this approach most often draws

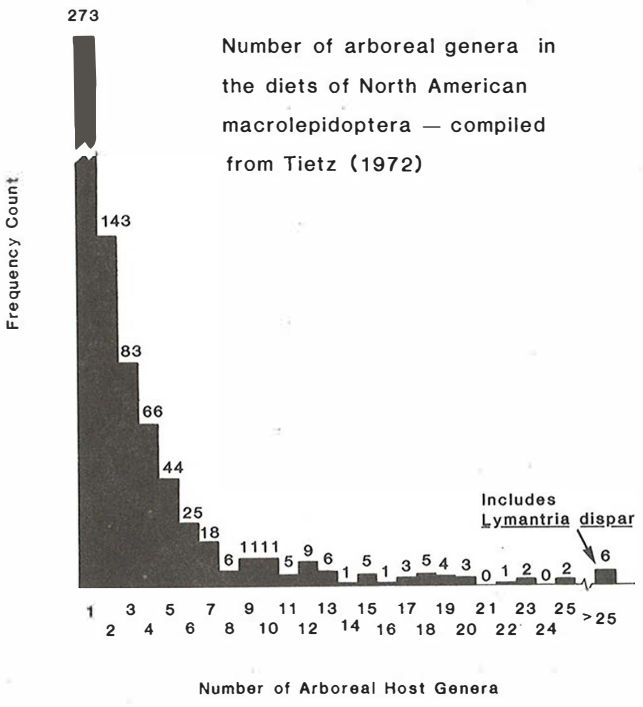

Figure 1. Numbers of genera of trees acceptable in the diets of North American macrolepidopterans; compiled from Tietz (1972).

on evidence from laboratory feeding trials and neurophysiological monitoring of sensilla exposed to test compounds. Dethier (1982) provides an interesting historical review of this literature. Ecological explanations focus attention on the nutritional quality of potential host foliage and assume that natural selection has led to preferences for hosts with relatively nutrient-rich foliage low in toxic or digestibility-reducing compounds. Although such ecological explanations have a long history (see Futuyma 1983 for a recent review) they received increased attention after Feeny (1976) and Rhoades and Cates (1976) independently proposed a general theory of plant defense against herbivores. These two types of explanation are not mutually exclusive; evolution should generally lead to proximate behavioral cues which result in larvae feeding on hosts of high nutritional quality.

In the work described in this paper I have taken an ecological rather than behavioral approach to attempt to understand the basis of larval host preferences in the gypsy moth. Working in a forest southeast of Montréal, Québec, which is near the northern limit of both the deciduous forest and the gypsy moth in North America, I initiated a long term study of gypsy moth host selection and of various tree characteristics which have been suggested to influence host selection by lepidopteran folivores. Here I describe the studied forest, summarize the history of its infestation by gypsy moth, explain the methods which have been used

TABLE 1. Phytosociological Summary of the Tree Stratum on the Southern Faces of Lake Hill, Mont. St. Hilaire, Québec.

Tree Species	Common Name	Acronym	Frequency[a]/	Density[b]/	Dominance[c]/	Relative Importance Value[d]/
Acer pensylvanicum L.	Striped maple	Apen	1	1	8.5	0.3
A. rubrum L.	Red maple	Arub	1	3	67.7	0.5
A. saccharum Marsh.	Sugar maple	Asac	24	158	2344.4	17.0
A. spicatum Lam.	Mountain maple	Aspic	1	4	39.2	0.5
Amelanchier sp.	Serviceberry	Amel	3	3	27.4	0.9
Betula papyrifera Marsh.	White birch	Bpap	9	47	696.3	5.5
B. lutea Michx. f.	Yellow birch	Blut	1	4	60.7	0.5
Carya cordiformis (Wang)K. Koch	Yellowbud hickory	Carya	2	2	35.6	0.6
Fagus grandifolia Ehrh.	Beech	Fagus	7	78	1373.2	7.6
Fraxinus americana L.	White ash	Frax	17	56	778.5	8.1
Juglans cinerea L.	Butternut	Jug	2	2	71.8	0.7
Ostrya virginiana (Mill.)K. Koch	Ironwood	Ostrya	20	181	1835.3	15.7
Pinus strobus L.	White pine	Pinus	3	4	92.4	1.1
Populus grandidentata Michx.	Big-tooth aspen	Pgran	2	11	206.1	1.4
Prunus pensylvanica L.f.	Pin cherry	Ppen	1	3	27.2	0.5
P. serotina Ehrh.	Black cherry	Pser	2	2	29.0	0.6
Quercus rubra L.	Red oak	Qrub	22	341	6963.8	33.3
Ulmus rubra Muhl.	Slippery elm	Urub	1	1	15.4	0.3
Tilia americana L.	Basswood	Tilia	12	22	357.5	4.7
Summations			131	923	15030.0	99.8

[a]/ Frequency: The number of 500 m^2 quadrats in which each tree species occurred; total sample was 24 quadrats.
[b]/ Density: The number of stems of each tree species found in all 24 quadrats.
[c]/ Dominance: The cumulative DBH in cm. for each tree species summed in all 24 quadrats.
[d]/ The mean of frequency, density, and dominance each relativized as a percentage of the respective total for all species; see Curtis (1959).

to quantify host preference, and detail the tree characteristics which were monitored over the period 1979 through 1981. I then present a preliminary analysis of these data and suggest a tentative explanation for the dynamics of the interaction between the gypsy moth and its host plants.

The Lake Hill Study Site

The work described here concerns a gypsy moth infested forest on Mont St. Hilaire, one of the eight Monteregian Hills which rise abruptly from the plains of the St. Lawrence River Valley in the vicinity of Montréal, Québec (Fig. 2). Mont St. Hilaire consists of seven low peaks surrounding a small lake; the peaks rise to a maximum of 416 meters, about 355 meters above the surrounding plain which is a mosaic of villages, agricultural land, and remnant woodland. The mountain itself is covered by forest which in many areas has been little or not at all disturbed for over 300 years; topographic and edaphic heterogeneity contribute to a diversity

Figure 2. Aerial view of Mont St. Hilaire, looking southeast toward Rougemont. Lake Hill rises from the south shore of Lac Hertel in the center of the figure. Photo courtesy of Dr. Luc Jobin, Laurentian Forest Research Centre, Ste. Foy, Québec.

of habitats including old growth beech-maple forests on deep moist soils, hemlock on steep rocky slopes, yellow birch-red maple swamps in depressions, oak-dominated forests on the dryer sites, and successional forests with aspen and birch on recently disturbed sites (Phillips 1972). Comparable forests have existed in this area for the past 8000 years (Richard 1977). Maycock (1961) provides a thorough summary of the geology, soils, climate, and flora of Mont St. Hilaire and Walther (1963) describes the vegetation of all the Monteregian Hills.

The forest in which gypsy moth activity has been primarily monitored is on the southern and western faces of Lake Hill, one of the lower peaks of Mont St. Hilaire which reaches an altitude of only 297 meters. The composition of this forest was determined by randomly placing twenty-four 500 m^2 circular quadrats along 4 altitudinal isoclines at about 25 m intervals down from the ridge top. In each quadrat the diameter at breast height (DBH) and the species of all trees (DBH $\geq$ 0.8 dm) were recorded. These data are summarized in Table 1. The relative importance values (Curtis 1959) emphasize the dominance of Quercus rubra, Acer saccharum, and Ostrya virginiana in this forest; Fraxinus americana, Fagus grandifolia, Betula papyrifera, and Tilia americana are also substantial components of the tree stratum but the remaining eleven tree species are of only minor importance. Tsuga canadensis, Populus tremuloides, P. balsamifera, P. deltoides and Betula populifolia occur sparsely on Lake Hill but were not found in the random quadrats.

Compared to the forests of the St. Lawrence Valley and southern Québec in general (Grandtner 1966; Bouchard and Maycock 1978) the Lake Hill forest is xeric. Detailed studies of the annual heat and water budgets of the south versus north slopes of Lake Hill are available (Rouse and Wilson 1969; Wilson 1970). The oak-dominated forest on the south slope is decidedly more prone to summer drought stress than the beech-maple forest on the north slope. Such topographic juxtaposition of mesic and xeric forest communities is common on the Monteregian Hills (Walther 1963). Xeric forests are generally more susceptible to attack by gypsy moth (Houston and Valentine 1977).

History of Gypsy Moth at Mont St. Hilaire

The gypsy moth appears to have first become established in Québec during the mid-1960's (Cardinal 1967; Brown 1967) and until the mid-1970's serious infestations were limited primarily to Huntingdon and Chateauguay counties south and west of Montréal (Martineau et al. 1975). About 1975 the zone of serious infestation began a steady expansion (Fig. 3); in 1975 traces of gypsy moth were noted on Mont. St. Gregoire, one of the Monteregian Hills south of Mont St. Hilaire (Martineau et al. 1976).

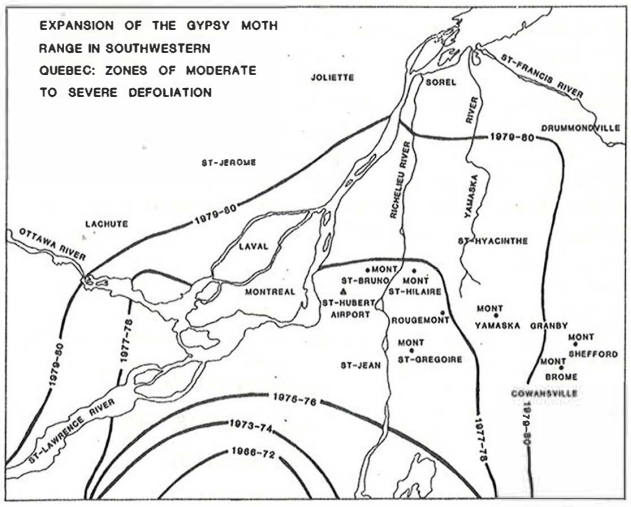

Figure 3. Approximate timing of expansion of the zone of serious gypsy moth infestation in Québec; adapted from information in Brown (1967), Cardinal (1967), Martineau et al. (1975, 1976), Lavallee et al. (1977, 1978), and Lachance et al. (1979, 1980, 1981).

There was no record of gypsy moth, and certainly had been no substantial defoliation, on Mont St. Hilaire until 1977 when 10 hectares of the forest on Burned Hill which is on the southwest face of the mountain were severely defoliated[1]/. It is likely that the infestation had been newly established only in the preceding few years; this slope of the mountain faces a public campground which may have been the source of infection through vehicular transport from areas to the south or west. By 1978 the infestation had spread to 259 hectares of which 195 were severely defoliated. This area included 123 hectares of the Lake Hill study site most of which was heavily defoliated in 1978. It is noteworthy that serious infestations were limited to the more xeric forests on Mont St. Hilaire in accord with Houston and Valentine's (1977) comments on the characteristics of sites most susceptible to gypsy moth infestations. As part of his doctoral research Madrid (1979; Madrid and Stewart 1981) monitored gypsy moth populations on Lake Hill in 1977 and 1978; his data provide a very useful supplement to my records which do not begin until 1979. In

[1]/ Jobin, L. (1978). Historique et situation actuelle de la spongieuse au Mont St. Hilaire, Internal report, Laurentian Forest Research Centre, Ste-Foy, Québec 13p.

addition government agencies[2]/ monitored the population on Lake Hill in 1978 and also in 1979 (Jobin 1982). Figure 4 summarizes the available information on gypsy moth population density at Lake Hill from 1977 through 1982. It is important to note that the population decline beginning in 1979 was not due to Québec's program of spraying Bacillus thuringiensis (Jobin 1982); the Lake Hill study site is on land owned by McGill University and protected as a UNESCO Man and Biosphere Ecological reserve in which spraying has not been allowed.

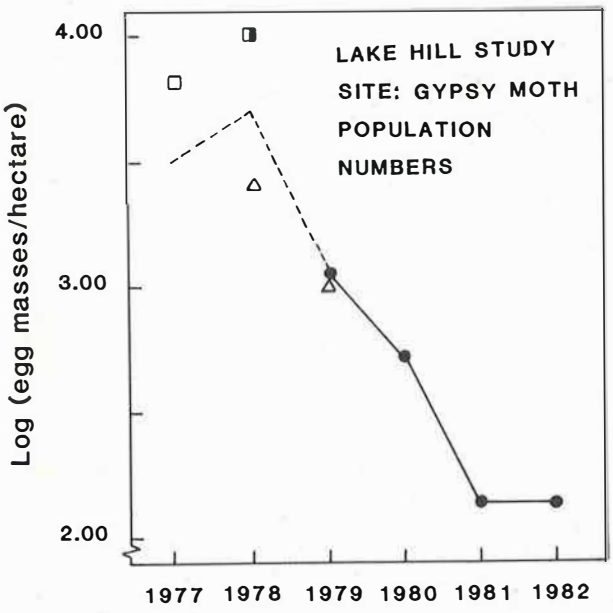

Figure 4. Gypsy moth population dynamics on Lake Hill. The squares are 1977 and 1978 data from Madrid (1979). The 1978 estimate by the government[2]/, shown as a half-closed square, is virtually identical to that by Madrid. The open triangles are data from Jobin (1982) in 1978 and 1979. All these plots were on the west end of Lake Hill, while my data (closed circles) also include the southern faces of Lake Hill.

Estimates of Gypsy Moth Host Preferences

The host preferences of late instar gypsy moth larvae on Lake Hill have been monitored from 1979 through 1982 using the method described in Lechowicz and Jobin (1983). This method measures preference as a function of the availability and the utilization of foliage on the different host trees in the forest. Emphasis is on the host preferences of late instar larvae which are primarily responsible for foliage losses (Valentine and Talerico 1980). If dispersing gypsy moth larvae actually had no preference for or against the foliage of a particular tree they would be expected to feed on that tree in direct proportion to its abundance in the forest canopy. This null expectation is founded on the assumptions that the probability dispersing larvae will encounter a host is determined by the host's relative abundance in the canopy and that larvae without preferences will settle on the first host they encounter. At dispersal larval preferences in the field should be closely related to the preferences reported in the behavioral literature which are determined in laboratory choice-trials (Mosher 1915; Barbosa et al. 1979). The late instar preferences reported here, however, arise not only from behavioral choices during dispersal but also from possible differences in early instar survival on different hosts. Larval survival may be controlled not only by foliage quality but also by bark roughness, canopy architecture, and similar traits that influence vulnerability to predators and parasites. These late instar host preferences are perhaps best viewed as measures of host susceptibility to defoliation by gypsy moth.

As discussed in detail by Lechowicz and Jobin (1983), the availability p_i for host i is measured by its contribution to the total DBH of the m different hosts in the sampled forest:

$$p_i = \sum_{j=1}^{n_i} b_{ij} \Big/ \sum_{i=1}^{m} \sum_{j=1}^{n_i} b_{ij} \qquad \text{eq.1)}$$

where b_{ij} is the DBH of the jth tree of species i. Utilization is estimated from the mean of repeated counts of numbers of late instar larvae congregating under tarpaper bands around each tree in the sampled quadrats; this is a standard method to estimate numbers of late instar larvae feeding on a tree (Weseloh 1974). This estimate assumes that late instar migration between trees does not occur during the counting period; in low density populations this assumption appears to be met (Lechowicz and Jobin 1983; Mauffette and Lechowicz[3]/; Wallner, this volume). The utilization r_i of host i is measured by the number of larvae on host i relative to the total number of larvae on all the sampled hosts:

2/ Bordeleau, C., C. Gagnon, C. Theriault, L. Jobin, C. Coulombe, and A. Caron (1980). Evaluation du programme de traitement au B.T. effectué contre la spongieuse au Québec en 1979, Internal Report, Ministre de Agriculture, Québec 37p.

3/ Mauffette, Y. and M.J. Lechowicz. The influence of host plant on the larval development rate of gypsy moth, Lymantria dispar (L.), in the forest environment, manuscript in review.

$$\underline{r}_i = \sum_{j=1}^{n_i} l_{ij} \Big/ \sum_{i=1}^{m} \sum_{j=1}^{n_i} l_{ij} \qquad \text{eq. 2)}$$

where l_{ij} is the mean number of larvae counted on the jth tree of species i.

Since gypsy moth larval growth and development differs on different host species (Schmidt 1956; Barbosa and Capinera 1977), the timing of larval counts to achieve a representative estimate of r_i is important. If a count is taken too early, larvae on some hosts will not have reached instar IV when the diurnal resting behavior on which the tarpaper counts depend begins (Leonard 1970). Conversely counts taken too late will miss larvae that have already pupated. Mauffette and Lechowicz[3] have analyzed the time course of larval numbers on 29 host species at 13 sites in southwestern Québec; in general there is about a 2 to 3 week window during which the mean of repeated counts will provide a representative estimate of late instar larval numbers across host species. It is desirable to make a fairly long series of counts and then discard the early and late entries which indicate that resting behavior is not developed on all hosts or that substantial pupation has occurred on some hosts. The preferences reported here are based on counts made on June 26-27 and July 3-4, 1979; on June 22 and 30, 1980; on June 21, June 29, and July 5, 1981; and on June 22, June 30, July 6 and July 14, 1982.

Several different algorithms are available to calculate preference from these measures of availability and utilization (Lechowicz 1982). Most give comparable results and differ primarily in convenience of interpretation. Here I have used Vanderploeg and Scavia's (1979a, 1979b) E* electivity index and their related selectivity index W. The selectivity for tree species i is:

$$W_i = (\underline{r}_i/\underline{p}_i) \Big/ \sum_{i=1}^{m} (\underline{r}_i/\underline{p}_i) \qquad \text{eq. 3)}$$

and the electivity for species i is:

$$E_i^* = (W_i - 1/n)/(W_i + 1/n) \qquad \text{eq. 4)}$$

where n is the number of potential host species. The selectivity W ranges from zero to one, a useful property in certain statistical analyses but not clearly indicative of preferred versus avoided hosts. In general, as a summary preference index, the E* electivity is easiest to interpret: E* is zero if the larvae feed randomly on a host, approaches minus one the more they avoid a host, and plus one the more they prefer a host. Lechowicz (1982) discusses the interrelationships and properties of all the available preference indices.

Monitoring of Host Foliage Characteristics

Many foliage characteristics have been implicated as possible factors determining the favorability of trees as hosts to lepidopteran folivores. Investigators have tended to focus on only one or a few factors in a given study despite the likelihood that a number of factors interact to control the susceptibility of a tree to herbivore attack. Certainly no single factor has proven to be even a reasonably universal predictor of herbivore susceptibility in woody plants. Also the predictable correlations between certain traits that may arise from constraints imposed by tree physiology and architecture can only be understood in a multifactorial analysis. Therefore within logistic limitations we have attempted to monitor a comprehensive set of foliage characteristics (Table 2) that may play a role in host selection by the gypsy moth. Sampling was concentrated on the spring foliage coincident with dispersal of gypsy moth and on the mid-summer foliage available to the late instar larvae. Samples were taken from a total of 23 tree species on Lake Hill but only 14 species both having adequate replication (3-6, mostly 5 or 6) and having been and having been included among the 19 species in the quadrats analyzed for host preference patterns are reported here. In the following paragraphs I briefly rationalize my choice of foliage characteristics and describe the methods used to assay them.

Leaf Toughness

Feeny (1970) demonstrated that the peak numbers of lepidopterans feeding on oak foliage coincided with the availability of tender, young leaves in the spring. For gypsy moth Hough and Pimental (1978) showed that larvae develop less well on the older, tougher leaves of host trees. Consequently toughness was monitored by Feeny's (1970) method which measures the mass required to shear the leaf tissue in an area between the main veins of the leaf. The shearing face of the penetrometer was 0.145 cm^2. In 1979 sand was used to add mass but subsequently water delivered through a pipette tip was found to give more reproducible results. Four replicate measurements of toughness were made on freshly harvested leaves.

Leaf Water Content

Scriber and Feeny (1979) have shown a correlation between higher leaf water content and better larval growth in lepidopteran larvae feeding on leaves of woody plants. Scriber and Slanksy (1980) review the importance of water content in effecting insect growth. The results of Hough and Pimental (1978) on gypsy moth larvae also indicate the favorability of high water content. The fresh and oven-dry weights of newly harvested leaves were used to calculate water content as a percentage of fresh weight at harvest; this is the normal practice in the entomological literature in contrast to the expression of water as a % dry weight common in the botanical literature.

Table 2. Foliage characteristics monitored from 1979 through 1981 at Lake Hill on Mont St. Hilaire, Québec. Rows designate date and Julian day of actual samples and the tabled entry indicates how samples were combined to represent spring or summer leaf condition in each year. Unsampled characteristics are indicated by n.d. In addition daily phenological records were kept in 1980 and 1981 during the period of canopy development.

	Toughness	% Water	% Nitrogen	Folin-Denis Phenolics	Precipitable Tannins	Leucoantho-cyanins	Leaf pH	Leaf Buffer Capacity
1979								
May 14 (Day 134)	spring	spring	spring	spring	n.d.	spring	n.d.	n.d.
May 21 (Day 141)	spring	spring	spring	spring	n.d.	spring	n.d.	n.d.
June 4 (Day 151)	spring	spring	spring	spring	n.d.	spring	n.d.	n.d.
July 18(Day 199)	summer	summer	summer	summer	n.d.	summer	n.d.	n.d.
1980								
May 27 (Day 148)	spring	spring	spring	spring	spring	spring	spring	spring
June 18(Day 170)	summer	n.d.	n.d.	summer	n.d.	summer	n.d.	n.d.
July 16(Day 198)	summer	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
1981								
June 1 (Day 152)	spring	spring	spring	spring	spring	spring	spring	spring

Leaf Nitrogen Concentration

McNeil and Southwood (1978) and Mattson (1980) review the considerable support for the critical importance of nitrogen availability to the growth of lepidopteran larvae feeding on the foliage of woody plants. The nitrogen concentration of oven-dry leaves was determined by a Kjeldahl analysis for total organic nitrogen (Bradstreet 1965) involving a sulfuric acid digestion in the presence of selenium catalyst and K_2SO_4 without any predigestion to reduce inorganic nitrogen. The resulting digest was then Nesslerized (Middleton 1960) and assayed colorimetrically for ammonia. Pace et al. (1982) have reported problems with nitrate reduction even in the normal Kjeldahl digestion but since tree leaves are extremely low in inorganic nitrogen (Van Tuil 1965) the nitrogen assayed here should be only that in forms available to lepidopteran larvae.

Leaf Concentrations of Various Phenolic Compounds

Many authors have taken the view that phenolic compounds function as important defenses against folivores, especially in woody plants (see particularly the reviews by Levin 1971; Feeny 1976; Swain 1978; Rhoades 1979; and Futuyma 1983). This view has not gone unchallenged, particularly by those who emphasize the many metabolic roles of phenolic compounds (Seigler and Price 1976) and those who question the efficacy of such putative defenses (Fox and McCauley 1977; Bernays 1978; Moran and Hamilton 1980; Martin and Martin 1983). This debate is aggravated by the extreme chemical diversity of phenolic compounds (Ribereau-Gayon 1972; Swain 1979) and the inadequacies of available assays for different groups of phenolic compounds. The latter problem has been recently reviewed but without a fully satisfactory conclusion (Horvath 1981; Martin and Martin 1982; Tempel 1982). Despite these problems, the unresolved controversy on the role of at least some types of phenolic compounds as defenses against herbivores requires their consideration here.

In the face of current methodological problems, I have settled on three assays for different phenolic fractions likely to have interpretable relationships with observed gypsy moth activity: 1) a Folin-Denis assay for total phenolics (Rosenblatt and Peluso 1941; Swain and Hillis 1959), 2) a leucoanthocyanin assay for condensed tannins (Swain and Hillis 1959 as modified by Govindarajan and Mathew 1965), and 3) a newly developed assay for phenolic compounds that bind to isinglass, a partially purified collagen from fish swim bladders often used to remove phenolic impurities from wine. The first two assays are well established. The isinglass assay is related to traditional tannin assays in the leather industry (Horowitz 1970), Marigo's (1972) absorption on gelatin, or Martin and Martin's (1982) recent modification of Bate-Smith's (1973) hemeanalysis. In all these methods Folin-Denis assays are made on an extract before and after exposure to a test protein to which tannins will bind, hopefully leaving only simple phenolics in solution. The difference in initial and final absorptance is then taken as a measure of biologically active tannins. Ideally the binding substrate should be

leaf protein from each of the tree species being studied (Martin and Martin 1983) but this is virtually impossible in most studies. Recent discussions (Martin and Martin 1982; Tempel 1982) agree that at least some type of precipitable tannin assay should be included in ecological studies because such an assay directly measures the ability of tannins to bind protein, the supposed basis of their role in plant defense. In all three of the assays used here I have expressed results as simple absorptance values for lack of appropriate calibration standards (Martin and Martin 1982). This does raise the practically unavoidable possibility in this cross-species comparison that absorptance will not be an unbiased quantitative index of actual phenolic concentrations because of qualitative differences in the absorption spectra of constituent phenolics on the different tree species.

One further aspect of these phenolic assays which has received too little consideration in the literature is the method of extraction of phenolic compounds from harvested leaf tissues. It is clear that different extraction solvents will differ in both the quantities and quality of phenolic compounds recovered (Ribereau-Gayon 1972). In 1979 we extracted 0.1 gr oven-dry (70-80°) weight of powdered leaf tissue with an 80% methanol acid 1% HCl solution for 24 hours in a soxhlet apparatus. In subsequent years the method of Swain (1979) was adopted in which 0.1 gr oven-dry (40-50° to lessen degradation of compounds during drying) weight of powdered leaf tissue was extracted three times in hot (80°) 50% methanol. Test extractions of fresh frozen rather than dried leaf tissue did result in higher absorption per unit dry weight in both the Folin-Denis and leucoanthocyanin assay but the readings were significantly positively correlated (FD: $r = 0.26$, $p = 0.029$; LA: $r = 0.35$; $p = 0.003$). The problems and potential errors inherent in taking truly parallel samples to estimate the equivalent dry weight of frozen samples makes the direct assay of dry tissue preferable in this comparative study.

Leaf pH and Buffer Capacity

Berenbaum (1980) has shown that caterpillar species feeding on leaves of woody plants have higher gut pH than those feeding on herbaceous plants. She reported a mean midgut pH of 8.67 for larvae feeding on woody plants, significantly higher than the pH 8.29 mean for species feeding on herbaceous foliage. She suggested that the high gut pH of caterpillars feeding on woody plant foliage would serve to break up tannin-protein complexes thus rendering the tannin-based leaf defenses postulated to be widespread in woody but not herbaceous plants less effective. On a dry weight basis the hydrolyzable tannins are considerably more effective at complexing with proteins than the condensed tannins (Swain 1978), but the hydrolyzable tannin-protein complexes are less stable than those formed by condensed tannins (Goldstein and Swain 1965). Dissociation of the tannin-protein complex occurs rapidly above pH 8 for condensed tannins and above pH 5 for hydrolyzable tannins (Loomis and Battaile 1966; Martin and Martin 1983). Thus high gut pH could conceivably increase the leaf nitrogen available to caterpillars feeding on woody plant foliage.

If this hypothesized mechanism is important in mediating the caterpillar-host tree interaction, trees that have lower leaf pH and/or higher leaf buffer capacity should be less preferred as hosts. Caterpillars would incur greater metabolic costs in maintaining their high gut pH to effectively digest more acidic and/or better buffered leaf tissue and should therefore tend to avoid such host foliage. To test this hypothesis I measured both the pH of freshly homogenized frozen leaf tissue and its buffer capacity as the µmoles NaOH necessary to bring the aqueous homogenate to pH 8.75.

Leaf Phenology

The temporal coordination of herbivore and host life cycles is obviously important, especially in insects like the gypsy moth which break diapause in concert with the emergence of the tree leaves on which they feed. Barbosa et al. (1979) have suggested that differences in tree phenology may influence susceptibility to attack by gypsy moth larvae. To test this hypothesis we made daily observations of canopy development on each tree from which leaves were harvested[4]/. Here the mean of the day a tree's first buds burst and the day 90% of its leaves had expanded was taken as a measure of the timing of its spring canopy formation.

Other Possible Factors

A considerable number of additional factors that might have some influence on gypsy moth host selection were not considered in these initial experiments. In some cases factors were rejected as of little or no importance on the basis of available evidence. Foliage concentrations of P, K, Mg, Na, Al, Ba, Fe, Sr, B, Cu, Zn, or Mn are unrelated to gypsy moth growth and fecundity (Barbosa and Greenblatt 1979; Valentine et al. 1983). Similarly variations in foliage concentrations of 25 amino acids were not correlated with gypsy moth success (Valentine et al. 1983). These investigators do report significant positive regressions of pupal weight on total free sugars and free sugar:Ca ratios; but the ranges in sugar and Ca concentrations sampled were based on both defoliated and undefoliated trees - other factors may well have contributed to these observed correlations. Most earlier reports (Beck and Reese

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[4]/ Lechowicz, M.J. The phenology of leaf emergence in a northern deciduous forest, manuscript in preparation.

1976; Scriber and Slansky 1981) indicated that foliage carbohydrate concentrations are adequate to meet insect requirements. Nonetheless, as discussed subsequently, some carbohydrate fractions may provide token cues important in host selection and, considering the recent results of Valentine et al., the possible importance of carbohydrates in gypsy moth nutrition cannot be dismissed.

Gypsy Moth Host Preferences at Mont St. Hilaires: 1979-1982

The larval host preferences of gypsy moth in the Lake Hill forest were generally stable during the decline of the outbreak in 1979 and 1980 (Fig. 5). Populus grandidentata, Quercus rubra, Ostrya virginiana, Amelanchier spp., and Acer saccharum were consistently preferred as larval hosts while Tilia americana, Carya cordiformis, Prunus pensylvanica, Fraxinus americana, Acer pensylvanicum, and Prunus serotina were consistently avoided. With the exceptions of Fagus grandifolia and Betula papyrifera, trees that had erratic electivity values during 1979-80 were poorly replicated in the available samples - Acer rubrum or Juglans cinerea, for example. The apparent drop in preference for beech in 1980 arises in part from a localized outbreak of nuclear polyhedrosis virus in a single quadrat; the increasing preference for white birch is an interesting but unexplained trend. In general the host preferences during this period of relatively high larval numbers are in accord with the earlier American and European reports reviewed by Lechowicz and Jobin (1983).

In 1981-82 when larval numbers had dropped to innocuous levels, there were some marked shifts in larval preference. Only Populus grandidentata was consistently strongly preferred over the 1979-82 interval. Quercus rubra and Ostrya virginiana, although still preferred, had lower electivity values in 1981 which returned toward their 1979-80 levels in 1982. Amelanchier dropped abruptly to being a slightly avoided host and Acer saccharum declined steadily to also being avoided in 1982. In contrast Fagus grandifolia which had been an avoided host became slightly preferred and Betula papyrifera had risen steadily until it was only slightly avoided. Most hosts avoided in 1979-80 such as Tilia americana and Fraxinus americana were even less preferred by the endemic larval population in 1981-82. There is some indication here that the few most preferred hosts are more heavily used by an endemic population and that the most avoided hosts are especially little used. Intermediate hosts seem to undergo shifts to greater or lesser preference that may potentially be explained by changes in foliage quality. It should be clearly recognized that even at innocuous population levels the gypsy moth population maintains a high degree of polyphagy with virtually all host species attacked to some degree.

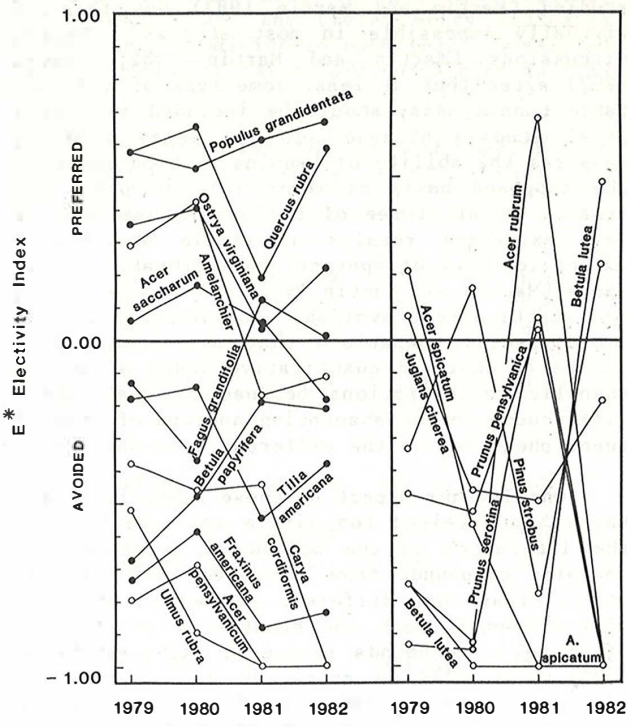

Figure 5. The host preferences of late instar larvae in the Lake Hill forest from 1979 through 1982. The calculations have allowed for occasional missing data; open circles represent electivity values based on fewer than 6 trees. Most of the poorly replicated host species are plotted in the right graph to avoid confounding the interpretation of trends in the generally better replicated species in the left graph.

Because of the inability of female gypsy moth adults to fly and the limited mobility of dispersing larvae (Mason and McManus 1981), these shifts in larval preferences may be explained in part by patterns of egg deposition rather than simply larval dispersal and host selection. It is useful to compare the observed electivities for numbers of egg masses on a host (calculated analogously to that for larvae) to the larval host preferences (Fig. 6). In general more preferred larval hosts also bear a greater proportion of the egg masses in the forest; this is not particularly surprising considering that selection should favor larval preferences for hosts which will allow successful survival and reproduction. It does suggest that late-instar migration to avoided larval hosts for pupation (Rossiter 1980; Mauffette and Lechowicz[5]) plays only a minor role in the population dynamics of gypsy moth on Lake Hill. On the other hand the cyclic tendencies apparent in the relationships between egg and larval host electivities supports the suggestion that changes in foliage quality may influence larval

host preferences. Consider, for example, Quercus rubra which had high larval and egg electivity in 1979; in 1980 larval activity was even slightly higher but egg electivity was sharply reduced. This reduction is reflected in a lowered larval electivity in 1981 but increased egg deposition. In turn by 1982 both larval and egg electivities have returned to 1979 levels. Such cyclic patterns raise the possibility that changes in foliage quality including induced responses such as those shown for birch, oak, and maple (Haukioja and Niemela 1979; Wallner and Walton 1979; Schlicting 1980; Schultz and Baldwin 1980) may influence the gypsy moth population dynamics on host trees from year to year.

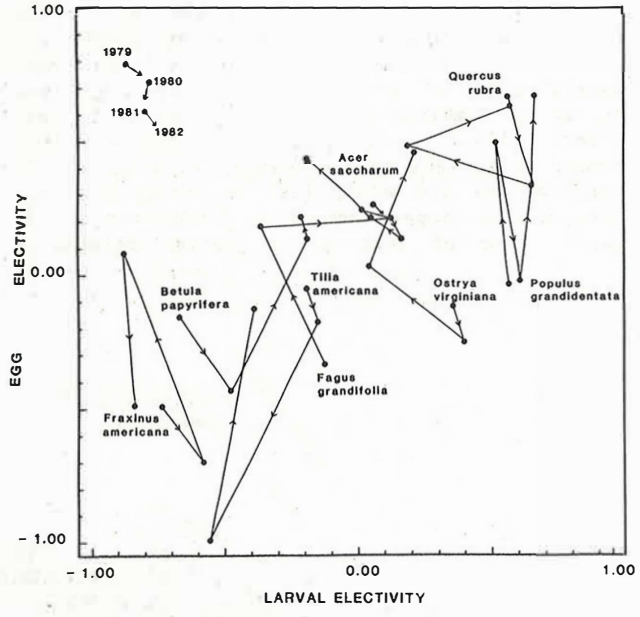

Figure 6. Electivity for egg masses versus that for late-instar larvae in the Lake Hill forest during 1979 through 1982. Trends are shown only for the eight well-replicated host species although all sampled hosts were used to calculate the electivities.

Foliage Characteristics at Mont St. Hilaire: 1979-1982

A multivariate approach to preliminary analyses of the gypsy moth host interaction. It is not possible in this paper to present the detailed results of all the assays of foliage quality in relation to gypsy moth host selection. Instead I have used a multivariate statistical technique that can most concisely be called biplot analysis (Gabriel 1971) to summarize the primary interrelationships between the measured foliage characteristics. Biplot analysis begins with a matrix of rows of objects described by columns of their attributes, in this instance 14 tree species characterized by their mean values for the traits in Table 2. The matrix is first relativized by dividing all entries by the maximum value in their respective columns. The relativized matrix is then centered by subtracting the respective column mean from each entry; this results in comparison of all tree species to a hypothetical, mean tree species. Finally this relativized and centered matrix is analyzed by canonical decomposition, a generalization of singular value decomposition, to acquire the best possible representation in few dimensions of the information in the multidimensional input matrix (see details in Gabriel 1971). The reduced matrix can then be represented graphically in two (hence biplot) or three dimensions to aid interpretation of trends in the data.

In interpreting a biplot such as that of the foliage traits analyzed here (Fig. 7) a number of general rules should be borne in mind. First consider the locations of the individual host species in the two-dimensional graph. Recall that the analysis is centered on a hypothetical mean host plotted at the origin - the dispersion of tree species around the origin is a graph of variation among hosts based on their foliage characteristics. Trees that are closer together are more similar than those further apart on the basis of the foliage traits used in the analysis.

Perhaps the most useful quality of the biplot compared to a technique like principal component analysis (Seal 1964) to which it is closely related is that unlike PCA the biplot also directly illustrates the contributions of individual traits in determining the relationships between trees. For convenience the traits are represented by vectors originating from the origin. The longer a vector, the more variable is that trait among the sampled trees - note however that small differences in a relatively invariant trait may still have important biological effects. The biplot shows only the pattern of variability in traits, the investigator must interpret that variation biologically.

Not only the length but also the direction of the trait vectors in the biplot are important aids to biological interpretation. The cosine of the angle between any two vectors approximates their correlation. Thus acute angles suggest positive correlation and obtuse angles negative correlation; trait vectors at right angles are uncorrelated.

Finally when any vector is extended across the biplot as an axis, the projections of tree species on that axis rank the trees from low to high in regard to that trait in the direction the vector points. In other words the vectors point in the direction that trees with high values of their respective traits will be dis-

5/ Mauffette, Y. and M. Lechowicz. Utilization of the larval host tree as a pupation site by the gypsy moth, Lymantria dispar L. (Lepidoptera: Lymantriidae), manuscript in review.

placed in the biplot; the actual placement of the tree species arises from the interaction of all the traits which "pull" the species in different directions with different strengths depending on its foliage characteristics.

A cautionary note is in order: like many other multivariate techniques, biplot analysis cannot fully represent all the information in a complex matrix in only a few dimensional graph. The accuracy of the interpretations just described hinges on the amount of variance in the original matrix represented in the biplot. Two vectors apparently highly positively correlated may, for example, actually diverge at a right angle in the third dimension. For this reason biplot analysis can only be an exploratory technique to provide initial help in puzzling out complicated and little known biological situations. It must be supplemented by careful scrutiny of actual correlation coefficients between traits and by traditional graphic comparisons of interrelationships between selected traits. As an exploratory technique biplot analysis can only suggest, not test, hypotheses. Given the large number of interacting traits which may influence gypsy moth host selection it does provide a useful and needed overview which helps focus future research on specific hypotheses involving fewer traits.

Biplot of Foliage Quality

The biplot of foliage traits alone (Fig. 7) emphasizes that many traits implicated in plant defense have fairly stable interrelationships with one another from year to year. For example, the suite of traits involving leaf acidity, buffer capacity, total phenolics, and precipitable tannins is notably stable both in spring and summer and from year to year. Trees with more acidic leaves tend to be consistently higher in total phenolic concentrations. Foliage toughness and water content are generally negatively correlated suggesting that these two traits which have usually been considered separately in the entomological literature may better be combined as a single measure of leaf sclerophylly. Leaf nitrogen concentrations remain relatively stable over time; although the correlations are weak, less sclerophyllous and less acidic leaves tend to be richer in nitrogen. Time of leafing out varies relatively

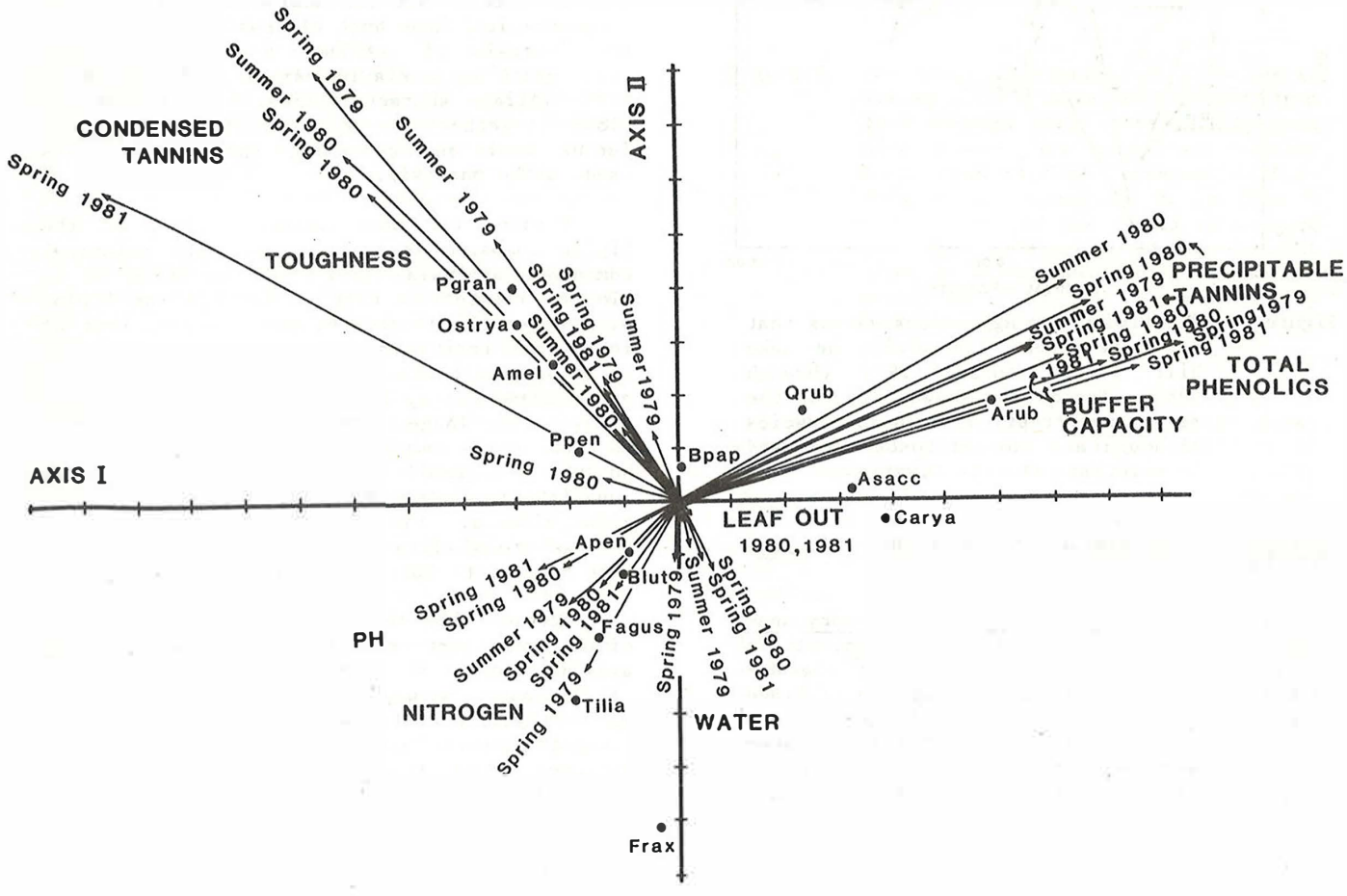

Figure 7. Biplot of mean foliage characteristics for 14 tree species in the Lake Hill forest. The two axes account for 70% of the variance in the relativized data matrix. See text for explanation of how to interpret this graph.

little among the 14 tree species on Lake Hill; actual values have a range of only 8 days in 1980 and 17 in 1981.

The annual pattern in condensed tannin concentrations is in contrast to the generally stable correlations among these other foliage characteristics. Only total phenolics and pricipitable tannins approach condensed tannins in terms of variation between trees. Unlike these other highly variable traits, condensed tannins also showed an interesting pattern of annual variation. During the outbreak year 1979 and 1980 the pattern of condensed tannin levels between tree species was similar and condensed tannins were higher in sclerophyllous leaves (Fig. 7). In 1981 as the gypsy moth population reached innocuous levels there was a shift in this pattern of condensed tannins in the spring leaves of the different host trees.

The host trees themselves fall along two general axes of variation in terms of the traits measured: 1) coordinated variation in a syndrome of traits involving highly intercorrelated changes in acidity, buffer capacity, total phenolics, precipitable tannins, and nitrogen and 2) in another syndrome involving toughness, water content, and condensed tannins. The distribution of tree species in the biplot suggests two relatively distinct modes of leaf phenolic metabolism. Some trees like Populus grandidentata, Ostrya virginiana, and Amelanchier are set apart by their relatively high concentrations of condensed tannins while others like Acer rubrum, A. saccharum, Carya cordiformis, and Quercus rubra have relatively low condensed tannin concentrations but high total phenolics and precipitable tannins. The general validity of these trends and their possible relevance to different modes of defense against folivores merit further consideration.

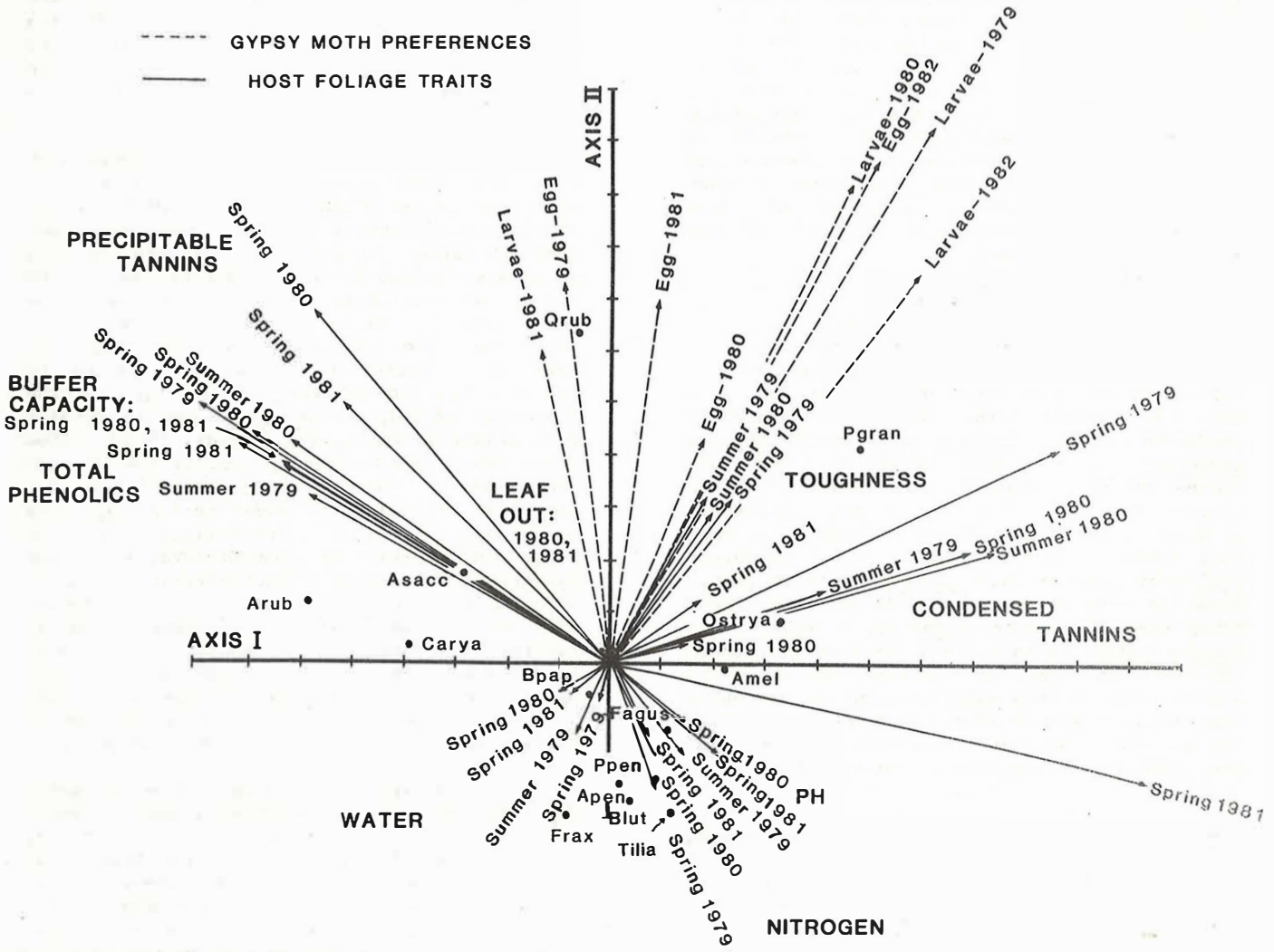

Figure 8. Second biplot including not only the plant traits in the preceding analysis (Fig. 7) but also the 1979 through 1982 larval and egg selectivities for the 14 host trees. Because interpretation of the biplot used here becomes difficult when a trait takes both positive and negative values, the selectivity W rather than the E* electivity values were used in this analysis. Lechowicz (1982) showed that W and E* are very highly correlated. The two axes account for 61% of the variance in the relativized data matrix. See text for further discussion.

Relationships of Gypsy Moth Activity to Foliage Quality

A second biplot (Fig. 8) adding the 1979 through 1982 larval and egg selectivity data for the 14 tree species to that on foliage quality was run to explore the correlations between these plant traits and the patterns of gypsy moth host preference. This biplot retains the underlying relationships of the plant traits among themselves. The two major axes of plant variation involving condensed tannins versus precipitable tannins and total phenolics are still apparent. Precipitable tannins, however, appear to be somewhat more associated with gypsy moth preferences than the other plant traits involved in the same syndrome of variation. Similarly sclerophylly, particularly in the summer, appears more associated with gypsy moth preferences than the concentrations of condensed tannins. Leaf pH, buffer capacity, total phenolics, and nitrogen appear to be only weakly or not at all related to larval host preferences. Although leaf phenology varies relatively little among hosts there is some indication that larvae may prefer hosts that leaf out later. In general this biplot suggests that dispersing gypsy moth larvae prefer trees that later in the season will have tough, dry leaf tissues and that these preferences may be modified in part by leaf concentrations of condensed and, to a lesser degree, precipitable tannins in the spring and early summer.

The actual distribution of host trees in the biplot also indicates that gypsy moth host preferences are not simply and entirely determined by the observed plant traits, but are also influenced by traits not included in this data set. For example, the two most consistently preferred hosts, Quercus rubra and Populus grandidentata, represent the two different syndromes of leaf types in the biplot of plant traits alone (Fig. 7). It is not immediately apparent what these two hosts have in common that leads to their being attacked preferentially by gypsy moth. Quercus rubra in particular is singled out as highly preferred from among trees like Acer saccharum, A. rubrum, and Carya cordiformis to which it is very similar in terms of the observed foliage traits. The biplot (Fig. 8) thus suggests that factors other than those traditionally supposed to determine susceptibility to herbivore attack among trees are important in gypsy moth host selection.

A Model of the Gypsy Moth-Host Tree Interaction

The diverse observational data analyzed here have allowed elimination of certain plant traits as uncorrelated with gypsy moth preferences and therefore unlikely to be important factors in host selection. On the other hand, although no clear and simple explanation of host selection has emerged, certain plant traits are implicated as factors involved in determining the probability that a tree will be attacked by gypsy moth. The recognition of such key traits in this exploratory analysis raises a number of hypotheses which require experimental tests. As a framework for continuing studies I have summarized these hypotheses in a tentative model of gypsy moth host selection which is explained below. The model has two main tenets: 1) that dispersing gypsy moth larvae preferentially settle on trees with higher sugar:tannin ratios in their young foliage and 2) that stress-induced variations in the sugar and tannin concentrations of young foliage can lead to year to year variation in a tree's susceptibility to attack by gypsy moth.

On a regional basis, the forests most susceptible to infestation by gypsy moth occur on more arid, nutrient-poor sites (Houston and Valentine 1977) where sclerophyllous tree species are most frequently found. Within these susceptible forests, host trees with more sclerophyllous mature foliage appear from the present analysis to be preferentially attacked by gypsy moth larvae. This positive association between sclerophylly and the host preferences of gypsy moth provides a useful clue to the possible basis of host selection by this polyphagous folivore.

Sclerophylly has long been associated with both arid, nutrient-poor environments and low rates of carbon fixation (Small 1973; Seddon 1974). Sclerophylly is believed to improve survival during the relatively frequent periods of stress typical of such habitats but at the expense of reduced productivity when conditions are favorable. In general we might expect the less productive sclerophyllous tree species to have more limited resources to allocate to defenses against folivores. In addition the leaves of sclerophyllous trees tend to develop more slowly in the spring (Federer 1976). Thus gypsy moth larvae feeding on the spring and early summer foliage of a sclerophyllous host may enjoy a relatively longer period of access to higher quality, immature foliage; models of gypsy moth larval development (Valentine and Talerico 1980) suggest that selection of hosts offering even slightly longer periods of favorable foliage availability can improve larval survival and fecundity. Host trees that later in the summer are most sclerophyllous and then apparently lowest in foliage quality may actually have provided the longest periods of immature foliage most favorable for larval development.

How then might dispersing larvae recognize the sclerophyllous hosts offering such a favorable opportunity for larval development? During larval dispersal all the available foliage is relatively tender and moist and there are no consistent correlations between the sclerophylly of young and old foliage; some cue other than sclerophylly itself must be used by the dispersing larvae. Soluble sugars, especially sucrose, which are known to be an important feeding stimulus in very many insects (Dethier 1982) seem the most likely proximate control on host selection by dispersing gypsy moth larvae. Transport of soluble sugars to developing tree

leaves is high (Dickson and Larson 1981) and would continue longer in the more slowly developing sclerophyllous species. Depending in part on the relative timing of eclosion and bud break, dispersing larvae will thus be more likely to encounter sugar-rich foliage on the slower-developing, sclerophyllous hosts. Further study is necessary to test this hypothesis that soluble sugar concentrations in host foliage during dispersal actually determine host selection.

Further investigations should also consider the possible interaction between soluble sugar and tannin concentrations. Dethier (1982) has reported that although gypsy moth larvae cannot sense tannic acid per se, this hydrolyzable tannin does suppress the larvae's electrophysiological response to sugars. Perhaps tannins alter the apparent levels of soluble sugars in the young foliage available to dispersing larvae. If this is the case we may hypothesize that gypsy moth preferentially attack trees that have high sugar:tannin ratios in their young foliage.

Tannins present in young foliage during larval development may also influence year to year trends in the numbers of dispersing larvae that potentially settle on different host trees. Because of the limited vagility of the later instars and female adults of the gypsy moth (Doane and McManus 1981; Wallner, this volume), any reduction in foliage quality on attacked trees will act to limit larval success on that tree and thereby reduce the local density of dispersing larvae the next year. Data for lepidopteran larvae including the gypsy moth (Feeny 1968; Karasov and Satarova 1973) have shown that tannins can reduce foliage digestibility. High tannin levels in the young foliage critical for larval development can thus reduce egg deposition by female larvae on these hosts. If in addition elevated levels of tannins can be maintained in young foliage the next spring, then the preference of dispersing larvae for the host may be further reduced by suppression of the neurophysiological response to sugar stimuli as hypothesized above. The maintenance of high tannin levels, however, depends on the availability of photosynthetic reserves which will tend to be lower in more sclerophyllous hosts. Sclerophyllous hosts will therefore tend to be more susceptible to sustained infestations of gypsy moth larvae from year to year. Moreover, productive hosts better able to either constitutively or facultatively maintain high levels of tannins in their spring foliage could actually shift large numbers of dispersing larvae to the less well-defended, sclerophyllous hosts. It is through mechanisms such as these that the gypsy moth preference for more sclerophyllous hosts may be expressed and maintained.

This model is in accord with the recent revival and elaboration (Haukioja 1980) of the idea that climatic stress on host plants can release a serious outbreak of insect herbivores. When all trees have been weakened by a stress such as a severe drought, limited reserves of photosynthate may be diverted from defense to other more essential functions. The polyphagous and widely dispersed gypsy moth larvae in the subsequent spring then would find an unusually high number of favorable host trees apparently high in sugar content for lack of masking tannins. Larval success on these drought stressed trees would be relatively high and defoliation would thus reduce the recovery of photosynthate resources even if climatic conditions were again favorable. Gradually enhanced defenses, probably aided by predator and pathogen attacks on gypsy moth (Doane and McManus 1981), would reduce the larval numbers to low enough levels for the normal patterns of leaf development and defense to prevail. The endemic gypsy moth population then would again preferentially attack the more sclerophyllous hosts which are generally less able to maintain effective tannin-based defenses and have the longer leaf development times favorable to gypsy moth larval success.

The model proposed here can potentially explain two key aspects of the gypsy moth-host interaction: 1) the basis of host selection and 2) the occurrence of periodic outbreaks. Additional observational and experimental tests are necessary to test its validity.

ACKNOWLEDGEMENTS

Many people have worked with me on this project. I want to especially thank Luc Jobin, Yves Mauffette, and the following laboratory and field assistants without whose help the project would have been impossible: Claude Blais, Patrick Blais, Pierre-Alain Blais, Anne Bruneau, Lyne Cossette, Susan Dudley, Ron Kara, Josée LaPierre, Dorothy Luk, Steve McCanny, David Moscovitz, Danielle Pouliot, Chantal Reid, Benoit St. Jacques, and Georgette Verebely.

A long term project like this would be difficult without the continued support of the staff at the McGill University Gault Estate and permission from the Gault Estate Board to work in the Scientific Reserve at Mont St. Hilaire. Funding from the Canadian National Sportsmen's Fund, the Laurentian Forest Research Centre of Environmental Canada, the Natural Sciences and Engineering Research Council of Canada, the McGill University Computing Centre, and Cornell University have supported this research. I am grateful to Brian Chabot, Paul Feeny, and Deborah Rabinowitz for providing a productive and stimulating environment during my stay at Cornell. Marcia Waterway, Bob Hagen, and Jean Chabot provided helpful critiques of the draft manuscript. Cathy Hughes prepared the camera ready copy.

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