

Estimating the susceptibility of tree species to attack by the gypsy moth, *Lymantria dispar*

MARTIN J. LECHOWICZ and LUC JOBIN* Department of Biology, McGill University, Montreal, Quebec, and *Laurentian Forest Research Centre, Environment Canada, 1080 rue du Vallon, Ste-Foy, Quebec, Canada

ABSTRACT. 1. Numbers of gypsy moth larvae feeding on each of 922 randomly sampled trees in a *Quercus–Acer–Fraxinus* forest in southwestern Quebec, Canada were counted in 1979 and in 1980 to quantify the larval feeding preferences as observed in the field for eighteen deciduous and one coniferous tree species at the northern range limit of the gypsy moth.

2. Both the diameter at breast height (dbh) and the estimated foliage biomass of the sampled trees were used to calculate the relative proportions of foliage represented by each of the nineteen tree species in the forest canopy. With these data on availability and utilization of the tree species by the gypsy moth larvae an Ivlev-type electivity index was used to quantify the larval feeding preferences. These preferences observed in the field define the susceptibility of a tree species to attack by the gypsy moth.

3. The feeding preferences calculated using estimated foliage biomass were comparable to the simpler calculation based on dbh (Spearman's $\rho = 0.79$; $P = 0.0001$). The dbh-based feeding preferences remained almost unchanged in 1979 and 1980 (Spearman's $\rho = 0.83$; $P = 0.0001$).

4. The composite 1979–80, dbh-based feeding preferences show *Quercus rubra*, *Populus grandidentata*, *Ostrya virginiana*, *Amelanchier* spp. and *Acer saccharum* were preferentially attacked by gypsy moth. *Prunus serotina*, *Betula lutea*, *Acer rubrum*, *A. pennsylvanicum*, *Fraxinus americana*, *Ulmus rubra*, *P. pennsylvanicum* and *B. papyrifera* were avoided. All nineteen tree species were, however, utilized to at least some degree by gypsy moth larvae.

5. These results quantitatively affirm and clarify earlier reports of gypsy moth feeding preferences in North America and Eurasia. The advantages and limitations of using an electivity index to estimate the susceptibility of different tree species to attack by folivores like the gypsy moth are discussed.

Key words. Electivity, feeding preference, polyphagy, herbivory, gypsy moth, *Lymantria dispar*, leaf allometry, dimensional analysis.

Introduction

The gypsy moth, *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae), has become a

Correspondence: Dr Martin J. Lechowicz, Department of Biology, McGill University, 1205 Avenue Docteur Penfield, Montreal, Quebec H3A 1B1, Canada.

major forest pest in northeastern North America (Leonard, 1974; Doane & McManus, 1981). Native to the deciduous and mixed forests of Eurasia (Giese & Schneider, 1979), the species was inadvertently introduced to North America at Medford, Massachusetts, in 1869 (Forbush & Fernald, 1896). Its North

American range has steadily expanded (USDA, 1972; Campbell, 1979) and now extends from southern Canada to southern Pennsylvania and from west central New York east to the Atlantic Ocean. In early feeding trials the gypsy moth larvae ate 458 of 477 eastern deciduous forest species (Forbush & Fernald, 1896). The polyphagous larvae feed primarily on the foliage of deciduous trees especially, members of the genera *Quercus* and *Populus* (Mosher, 1915; Campbell & Sloan, 1977a; Doane & McManus, 1981). Gypsy moth infestations, which undergo periodic outbreaks (Campbell & Sloan, 1977b, 1978a, b), result in the lowered growth and survival of attacked trees (Campbell, 1979; Wargo, 1978; Doane & McManus, 1981). Because of the feeding preferences of the larvae, tree species are differentially susceptible to the deleterious consequences of gypsy moth defoliation.

Early reports of gypsy moth feeding preferences were largely based on laboratory trials supplemented by anecdotal field observations (Forbush & Fernald, 1896; Mosher, 1915). Mosher, for example, recorded larval growth and survival in the laboratory on diverse foliage samples that were frequently renewed with fresh collections from the field. He also conducted pairwise choice trials for many foliage samples. Mosher then subjectively classed 147 woody species as highly favoured (42), favoured in later instars (13), not favoured but eaten (32) and unfavoured (60). His classification, which has been used essentially unchanged even in very recent studies (Campbell & Valentine; 1972; Houston & Valentine, 1977; Valentine & Houston, 1979), suffers from a number of deficiencies. First, this simple quartile classification does not allow the precise interspecific discrimination desirable for many contemporary applications. Second, because of both post-harvest and seasonal shifts in leaf composition the relevance of Mosher's laboratory trials to events in the forest can be questioned. Finally, laboratory feeding trials in general cannot provide sound estimates of tree susceptibilities to herbivore attack. A tree preferred in a laboratory trial may not, for example, be utilized because it typically grows in sites microclimatically unsuited to gypsy moth or not conducive to colonization by the dispers-

ing larvae (see Barbosa, 1978a; Lance & Barbosa, 1981).

Campbell & Sloan (1977b) recently proposed a defoliation ratio based on field data which circumvents the problems inherent in Mosher's laboratory study. Campbell & Sloan analysed data on gypsy moth defoliation levels for sites throughout central New England. The mean defoliation for each of thirty-seven tree species was compared as a ratio to the defoliation of *Quercus alba*. While these defoliation ratios improve considerably on earlier efforts, their general applicability even within central New England is compromised by a failure to account for the relative abundances of tree species in the sampled forests. Futuyama & Wasserman (1980) have shown that forest composition and herbivore feeding preferences can interact to influence defoliation levels on different tree species. Mauffette (1982) found that gypsy moth utilization of both preferred and avoided tree species increased with the tree's relative abundance in the attacked forest. A field based index of gypsy moth feeding preferences which takes account of forest composition at the sampling sites would be a useful improvement over currently available measures.

This paper proposes a method to determine such an index of gypsy moth feeding preference. With appropriate modification of the herbivore census techniques, the index can be calculated for any leaf-feeding herbivore.

Methods

An ideal index of feeding preference would measure the degree to which the foliage of a tree species is utilized relative to its abundance in the forest. In the simplest analysis, a herbivore feeding at random (exercising no preference) should consume the foliage of a particular tree species in direct proportion to the tree's relative abundance. Any significant deviations from this random model suggest that the gypsy moth larvae have preferentially chosen or avoided the tree species on which to feed and live during larval development. An appropriate algorithm can then be used to express those deviations as an index of feeding preference for each tree species in the forest.

Lechowicz (1982) reviewed a family of such algorithms, all derived from Ivlev's (1961) classic electivity and forage ratio indices, and recommended the use of Vanderploeg & Scavia's (1979a) relative electivity, E^* , to quantify gypsy moth feeding preferences.

Following Vanderploeg & Scavia (1979a, b) the preference or electivity E_i^* for a particular host tree species i is calculated as follows:

$$E_i^* = (W_i - 1/n)/(W_i + 1/n) \quad (1)$$

where n is the number of host tree species available in the forest and W_i is the selectivity coefficient calculated as:

$$W_i = \frac{E_i'}{\sum_{i=1}^n E_i'} \quad (2)$$

Here E_i' is Ivlev's (1961) forage ratio for tree species i , the proportion of species i that has been eaten relative to the proportion available:

$$E_i' = r_i/p_i \quad (3)$$

where

r_i = the proportion of the total gypsy moth diet represented by tree species i ,

p_i = the proportion represented by tree species i of the total foliage biomass available in the forest.

By standardizing the forage ratios to a scale from 0 to 1, the selectivity coefficient, W_i , provides for meaningful between plot comparisons of preference. This generality is further improved by considering the number of tree species in the sampled forest to adjust the range of E^* . The E^* index ranges from +1 (completely preferred) to -1 (completely avoided). Lechowicz (1982) discusses the sampling behaviour and interpretation of the E^* index at all combinations of r and p .

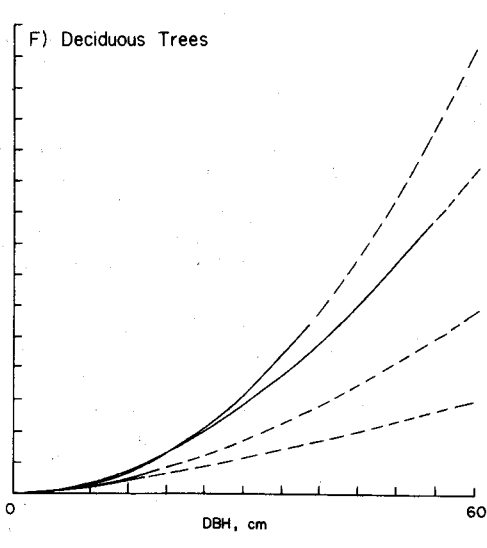
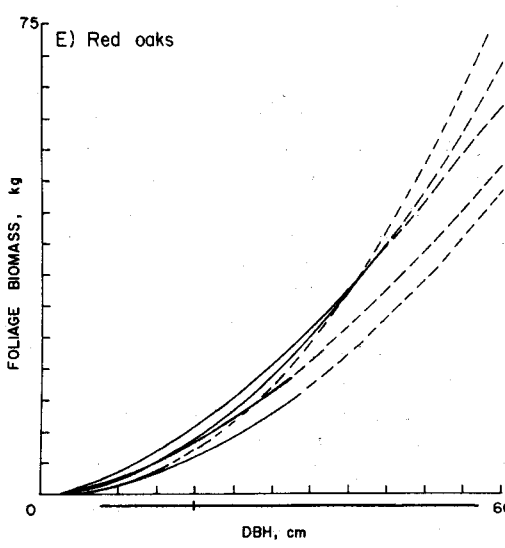
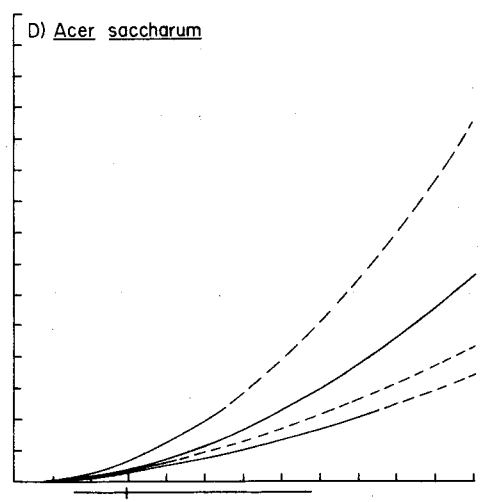
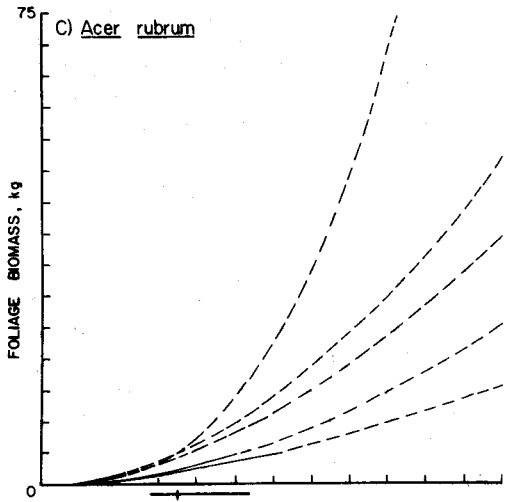
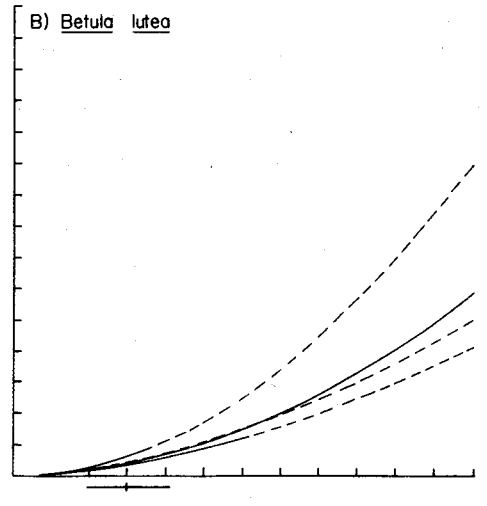
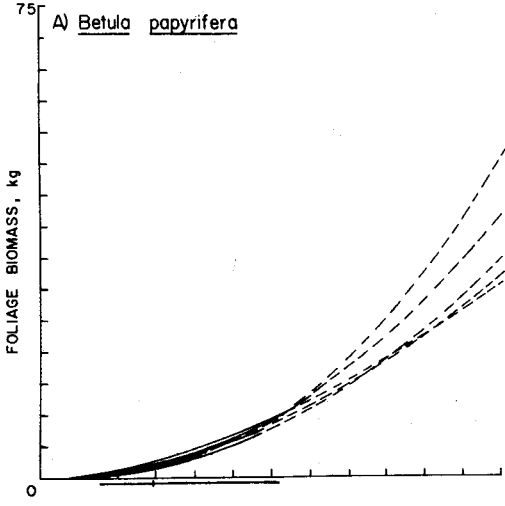
The proportion of the forest's foliage biomass represented by species i , p_i in the calculation of E_i' , can be estimated by the techniques of dimensional analysis developed for studies of forest productivity (Whittaker & Marks, 1975). By destructive harvest of a representative sample of individual trees, the allometric relationship between foliage biomass and trunk diameter at breast height (dbh, traditionally measured at 1.4 m) can be

determined by regression. Forest composition is sampled by appropriately stratified, random quadrats (Greig-Smith, 1964). Each individual tree's foliage biomass is estimated from its dbh using available regressions for that species to calculate:

$$p_i = \frac{\sum_{j=1}^n b_{ij}}{\sum_{i=1}^m \sum_{j=1}^n b_{ij}} \quad (4)$$

where b_{ij} is the calculated foliage biomass for j th of n trees of the i th among m tree species. As a simpler alternative, if suitable allometric relationships are unavailable, an analogous estimate of p_i can be made using dbh directly (Lechowicz, 1982). Fig. 1 illustrates some of the allometric relationships in the literature; Table 1 gives the sources of all the relationships used in this analysis. In this paper p_i is estimated from both estimated biomass and measured dbh to compare the utility of the two approaches.

The estimation of the proportion of the total gypsy moth diet represented by tree species i , r_i in the calculation of E_i' , is simplified by a number of aspects of gypsy moth biology. The female gypsy moth is incapable of flight, and host selection is affected by wind-dispersed early instar larvae (Leonard, 1971; Capinera & Barbosa, 1976; Lance & Barbosa, 1981). Within limits of food reserves (3–5 days according to Forbush & Fernald, 1896) wind-dispersal continues until a suitable host is found. Except at unusually high population density, beginning in the third and fourth instar larvae feed at night and rest by day under bark flaps or similar shelters on or near the tree (Leonard, 1970). By placing a skirt of tarpaper around the tree at breast height the larvae feeding on the tree hide in this artificial shelter and can be counted during the day (Weseloh, 1974). Odell & Godwin (1979) found that 95% of the larvae feeding on *Quercus velutina* congregated under similar artificial resting sites. Lance & Barbosa (1982) report that late instar larvae do migrate from tree to tree but remain longer on trees with both preferred foliage and sufficient daytime resting sites. Migration is greatest in high density infestations but does occur in endemic



populations like the one sampled here. The tarpaper skirts provide comparable resting sites on all sampled trees and minimize the effects of physiognomic differences between trees on our estimate of preference. Larval counts on each tree in the sampled quadrats can be used to calculate r_i for the gypsy moth population as:

$$r_i = \frac{\sum_{j=1}^n l_{ij}}{\sum_{i=1}^m \sum_{j=1}^n l_{ij}} \quad (5)$$

where l_{ij} is the number of larvae observed on the j th of n trees of the i th among m tree species. Feeding preference is expressed primarily in the first instar and counts of third to fifth instar larvae may therefore include some bias reflecting differential early instar mortality between tree species. Bess (1961) reports 5 year mean mortalities in three Connecticut forests as 25.6% in the first stadia, 23.2% in the second, 28.3% in the third and 31.2% in the fourth. The possible bias arising from differential mortality is in part discounted by the far greater defoliation caused by a later instar larva (Forbush & Fernald, 1896; Braham & Witter, 1978). Feeding preferences of later instar larvae thus better reflect a tree's susceptibility to loss of foliage through gypsy moth defoliation.

These estimates of r and p were calculated for a forest protected as a research preserve at Mont St Hilaire in southwestern Quebec (45° N, 73° W; see description in Maycock, 1961). Gypsy moth first colonized Mont St Hilaire in 1977 and by 1978 the infestation had spread to 259 ha (Jobin, 1978). Madrid (1979) and Bordeleau *et al.* (1980) review aspects of the biology of these infestations on Mont St Hilaire.

We established twenty-four circular quadrats, each of 500 m², randomly along four approximately equally spaced altitudinal isoclines on the south-facing slopes of Lake Hill

at Mont St Hilaire. In May 1979 each of the 922 trees (dbh ≥ 8.0 cm) in these quadrats was identified and its diameter at breast height tallied. The sampled forest was dominated by *Quercus rubra*, *Acer saccharum* and *Ostrya virginiana* with a substantial admixture of *Fraxinus americana*, *Fagus grandifolia*, *Betula papyrifera* and *Tilia americana* (see Table 1). To allow for different larval development rates on different host trees (Mauffette, 1982) replicate larval counts on the 922 trees were taken on 26–27 June and 3–4 July 1979 and on 23 June and 1 July 1980. In 1979 there were 1280 and in 1980 517 eggs masses/ha found at the Lake Hill site. Bess (1961) reports populations in New England forests frequently ranging up to 325 egg masses/ha and as high as 3200 egg masses/ha. The low to moderate infestation levels and the lack of substantial canopy loss on Lake Hill both suggest that neither excessive mortality nor excessive larval migration confounded the calculation of E^* .

Results

Using the χ^2 test described in Lechowicz (1982), it is evident that the gypsy moth larvae were not feeding at random in either year based on either estimated foliage biomass or measured dbh ($P < 0.001$ in all four cases). In 1979 estimates of E^* based on measured dbh showed *Populus grandidentata*, *Quercus rubra*, *Ostrya virginiana*, *Acer saccharum*, *A. spicatum*, *Amelanchier* spp. and *Juglans cinerea* to be preferentially attacked by gypsy moth (Fig. 2). The sample sizes for the latter three species are small (Table 1). *Prunus serotina*, *P. pensylvanica*, *Fraxinus americana*, *Acer pensylvanicum*, *A. rubrum*, *Betula lutea*, *B. papyrifera* and *Ulmus rubra* were strongly to moderately avoided. The 1979 estimates of E^* based on estimated foliage biomass are broadly similar to those based on dbh with a number of notable exceptions (Fig. 2). *Quercus rubra* surprisingly is no longer shown

FIG. 1. Allometric relationships between the dry weight of foliage in kg and diameter at breast height (dbh) in cm from regressions in the literature for: (A) *Betula papyrifera*, (B) *B. lutea*, (C) *Acer rubrum*, (D) *A. saccharum*, (E) *Quercus* spp., section *Erythrobalanus*, and (F) composites of 'all deciduous trees'. The literature sources for each relationship appear in Table 1. Broken lines are extrapolations beyond the data used to create the published regression. The cross under the abscissa in figures A–E indicates the mean and range of dbh in the sampled trees on Lake Hill.

TABLE 1. Forest composition in 1979 and larval distribution in 1979 and 1980 on the south-facing slopes of Lake Hill, Mont St Hilaire, Quebec.

Species	Acronym	n	Mean 1979 dbh (cm)	1979 range of dbh (cm)	Summed no. of larvae*		Summed 1979 estimates of ldw (kg)	Sources of algorithms used to estimate ldw
					1979	1980		
<i>Acer pensylvanicum</i> L.	Ap	1	8.5	-	0.5	1.0	0.52	Whittaker <i>et al.</i> (1974)
<i>A. rubrum</i> L.	Ar	3	22.6	19.0-27.7	5.0	1.5	200.82	Reiners (1972); Crow (1977); Kinerson & Bartholomew (1977); Ribe (1979); Ker (1980a)
<i>A. saccharum</i> Marsh.	As	158	14.8	8.0-38.7	1342.0	1973.5	430.83	Whittaker <i>et al.</i> (1974); Reiners (1972); Crow (1977); Kinerson & Bartholomew (1977); Ribe (1979); Ker (1980a)
<i>A. spicatum</i> Lam.	Asp	4	9.8	9.3-10.5	23.5	5.0	2.66	Whittaker <i>et al.</i> (1974)
<i>Amelanchier</i> spp.	Am	3	9.1	8.5-9.6	25.5	40.5	1.23	Reiners (1972)
<i>Betula papyrifera</i> Marsh.	Bp	47	14.8	8.0-31.3	69.0	154.0	119.44	Whittaker <i>et al.</i> (1974); Reiners (1972); Crow (1977); Ribe (1979); Ker (1980a)
<i>B. lutea</i> Michx. f.	Bl	4	15.2	9.9-20.2	4.5	0.0	10.45	Reiners (1972); Whittaker <i>et al.</i> (1974); Ribe (1979); Ker (1980b)
<i>Carya cordiformis</i> (Wang.) K. Koch	Cc	2	17.8	9.1-26.5	8.0	8.0	13.90	Blackman & Ralston (1968)
<i>Fagus grandifolia</i> Ehrh.	Fg	77	17.7	8.0-45.0	538.0	388.0	287.56	Whittaker <i>et al.</i> (1974); Ribe (1979); Ker (1980b)
<i>Fraxinus americana</i> L.	Fa	56	13.9	8.0-39.3	58.0	128.5	93.65	Ker (1980b)
<i>Juglans cinerea</i> L.	Jc	2	35.9	18.3-53.5	42.0	16.5	55.06	Blackman & Ralston (1968)
<i>Ostrya virginiana</i> (Mill.) K. Koch	Ov	181	10.1	8.0-21.6	1937.0	2489.0	176.32	Reiners (1972)
<i>Pinus strobus</i> L.	Pst	4	23.1	21.2-26.0	23.5	85.0	32.78	Kittredge (1944); Ker (1980b)
<i>Populus grandidentata</i> Michx.	Pg	11	18.7	11.8-27.8	382.5	404.0	23.56	Koerper & Richardson (1980)
<i>Prunus pensylvanica</i> L.f.	Pp	3	9.1	8.0-10.5	3.5	3.5	4.68	Ribe (1979)
<i>P. serotina</i> Ehrh.	Ps	2	14.5	11.0-18.0	0.5	1.0	8.22	Ribe (1979)
<i>Quercus rubra</i> L.	Qr	341	20.4	7.9-56.3	12896.5	19809.5	3487.75	Rothacher <i>et al.</i> (1954); Whittaker & Woodwell (1968); Blackman & Ralston (1968); Kinerson & Bartholomew (1977); Reiners (1972)
<i>Ulmus rubra</i> Muhl.	Ur	1	15.4	-	2.5	0.5	2.96	Monk <i>et al.</i> (1970); Blackman & Ralston (1968); Kinerson & Bartholomew (1977); Ribe (1979)
<i>Thuja americana</i> L.	Ta	22	16.2	8.4-34.8	123.5	160.0	320.90	Blackman & Ralston (1968); Kinerson & Bartholomew (1977); Ribe (1979)

* 1979 mean based on counts made 26-27 June and 3-4 July 1979; 1980 mean based on counts made 23 June and 1 July 1980.
 † One windthrown oak, 24.5 cm dbh, was omitted from the 1980 calculations.

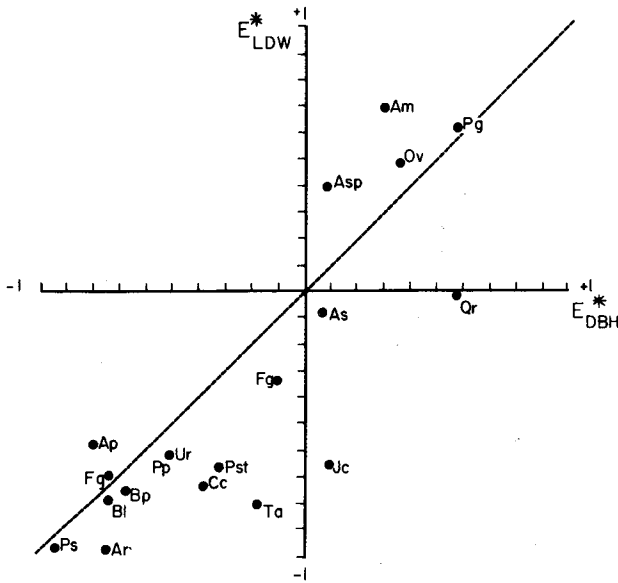


FIG. 2. The relationship between the 1979 E^* index of gypsy moth feeding preferences calculated on the basis of measured dbh (ordinate) versus estimated foliage biomass (abscissa). See text for details. The species acronyms appear in Table 1. A species would fall on the diagonal line if the two calculation methods gave identical results.

to be preferred, *Amelanchier* is somewhat more preferred and *Juglans cinerea* appears to be strongly avoided. *Tilia americana*, *Pinus strobus* and *Carya cordiformis* have shifted

from weakly to strongly avoided. Overall estimates of E^* based on either foliage biomass or dbh give comparable results for thirteen of the nineteen sampled tree species;

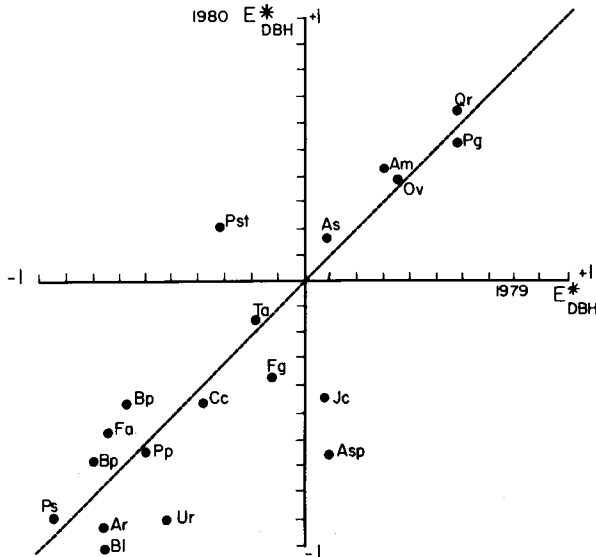


FIG. 3. The relationship between the 1979 (ordinate) and 1980 (abscissa) E^* index of gypsy moth feeding preferences. See text for details. The species acronyms appear in Table 1. A species would fall on the diagonal line if it did not differ in the two years.

TABLE 2. Composite 1979–80 E^* index of gypsy moth feeding preferences in southwestern Quebec compared to Campbell & Sloan's (1977) Defoliation Ratio for New England. The table is in order of decreasing preference.

Species	Common name	E^*	Defoliation ratio
<i>Quercus rubra</i>	Northern red oak	0.622	0.90
<i>Populus grandidentata</i>	Largetooth aspen	0.554	1.06
<i>Ostrya virginiana</i>	Ironwood	0.376	0.64
<i>Amelanchier</i> spp.	Serviceberry	0.375	—
<i>Acer saccharum</i>	Sugar maple	0.128	0.18
<i>Pinus strobus</i>	Eastern white pine	0.035	0.31
<i>Juglans cinerea</i>	Butternut	-0.146	—
<i>Tilia americana</i>	Basswood	-0.160	1.12
<i>Acer spicatum</i>	Mountain maple	-0.202	—
<i>Fagus grandifolia</i>	Beech	-0.235	0.45
<i>Carya cordiformis</i>	Bitternut hickory	-0.418	0.30
<i>Betula papyrifera</i>	White birch	-0.547	0.68
<i>Prunus pensylvanica</i>	Pin cherry	-0.619	0.17
<i>Fraxinus americana</i>	White ash	-0.641	0.06
<i>Ulmus rubra</i>	Slippery elm	-0.698	0.48
<i>Acer pensylvanicum</i>	Striped maple	-0.722	—
<i>A. rubrum</i>	Red maple	-0.839	0.38
<i>Betula lutea</i>	Yellow birch	-0.873	0.24
<i>Prunus serotina</i>	Black cherry	-0.910	0.40

the Spearman rank correlation between the two estimates in 1979 is 0.79 ($P=0.0001$).

The dbh-based estimates of E^* for 1979 and 1980 were used to examine annual variation in the observed feeding preferences (Fig. 3). Compared to 1979, *Juglans cinerea* and *Acer spicatum* were conspicuously not preferred. *Ulmus rubra* shifted from moderately to strongly avoided. *Pinus strobus* shifted from moderately avoided to moderately preferred. The sample size for all four species was small (Table 1). The actual proportions of larvae feeding on the nineteen tree species in 1979 versus 1980 differ significantly ($P < 0.001$) by the χ^2 test described in Lechowicz (1982). This difference arises primarily from the decreased use of *Acer spicatum*, *Fagus grandifolia*, *Juglans cinerea* and *Populus grandidentata* and increased use of *Pinus strobus* and *Quercus rubra* in 1980. When these shifts in utilization are considered in relation to the trees' relative abundances, the correspondence in feeding preferences between the two years remains very good as indicated in Fig. 3. The Spearman rank order correlation between the 1979 and 1980 dbh-based estimates of E^* is 0.83 ($P=0.0001$).

The 1979–80 composite E^* values (Table 2) may be taken as a summary measure of

gypsy moth feeding preferences at Lake Hill. *Quercus rubra*, *Populus grandidentata*, *Ostrya virginiana*, *Amelanchier* spp. and *Acer saccharum* are preferentially attacked by the gypsy moth. *Prunus serotina*, *Betula lutea*, *Acer rubrum*, *A. pensylvanicum*, *Fraxinus americana*, *Ulmus rubra*, *P. pensylvanicum* and *B. papyrifera* are avoided. It should be noted that all nineteen species were utilized to at least some degree by the polyphagous larvae.

Discussion

For a folivore like the gypsy moth, the calculation of an index of feeding preference like E^* makes the most conceptual sense if based on its food resource: foliage biomass. The relative availability of the host species can then be taken as directly proportionate to each tree species' contribution to the total foliage biomass in the forest canopy. Unfortunately two practical problems inherent in estimating foliage biomass essentially preclude its use in calculating E^* : (1) the allometric data necessary to estimate foliage biomass from more readily measured variables like tree height and diameter are difficult to obtain, and (2) site to site variation in a species leaf

allometry can introduce bias when published data are applied at a new site.

Allometric relationships are available for many but not all tree species (Tritton & Hornbeck, 1982). For example, despite concerted effort no data on the allometry of *Tilia americana*, an important forest tree, could be found. Determining unavailable allometric relationships is impractical (see Alemdag, 1980), yet the substitution of relationships for related taxa or 'all deciduous trees' may bias subsequent calculations of feeding preference. Even when allometric relationships for a species are available, site to site variation in canopy architecture can confound the estimation of foliage biomass. Koerper & Richardson (1980), for example, report significant differences in allometry for *Populus grandidentata* as a function of site quality. The broad range of foliage biomass estimates apparent in the literature for a given dbh (see Fig. 1) also reflect this problematic site to site variation in allometry. Because of these difficulties in estimating foliage biomass, the calculation of E^* feeding preferences directly with the untransformed dbh measurements is the pragmatic and sound alternative. The remainder of this discussion will consequently emphasize the dbh-based estimates of E^* found on Lake Hill in 1979 and 1980.

The annual variation in gypsy moth feeding preferences was not significant (Fig. 3). The 1980 samples were slightly later in the gypsy moth development cycle than those in 1979. This could explain the apparent preference for *Pinus strobus* since larvae have been reported to congregate on conifers in the last instar. Such migration to alternate hosts by late instar larvae appears to confer increased resistance to pathogens (Rossiter, 1981). Greater larval mortality on *Juglans cinerea* and *Acer spicatum* in the later sample may explain the apparent avoidance of these species in 1980. All these species were represented by only a few trees in our samples and the observed annual variations in feeding preference may simply be sampling artefacts. As a more robust basis for further discussion the 1979 and 1980 data have been merged to calculate a composite estimate of gypsy moth feeding preferences on Lake Hill (Table 2).

Members of the genera *Quercus* and *Populus* have been generally acknowledged as among

the most preferred hosts of gypsy moth in North America (Houston & Valentine, 1977; Campbell & Sloan, 1977a; Barbosa, 1978b). European workers also frequently identify species of *Quercus* and *Populus* as among the most preferred hosts for gypsy moth (Kurir, 1953; Györfi, 1960; Kuseva, 1964; Varga, 1969; Maksimovic & Politeo, 1970; Marcu, 1972; Fratian, 1973). The high E^* values for *Quercus rubra* and *Populus grandidentata* in the Lake Hill gypsy moth population provide a quantitative affirmation of these earlier reports.

The observed preferences for *Ostrya virginiana*, *Amelanchier* spp. and *Acer saccharum* illustrate the power of electivity indices to identify preferential feeding on the rarer or less completely utilized tree species. *Ostrya virginiana* has been recognized as a food of intermediate value utilized by a small proportion of the population (Mosher, 1915; Campbell & Sloan, 1977a). On Lake Hill the gypsy moth clearly utilizes *Ostrya* in excess of its availability in the forest — the species is a preferred food. This preference may reflect similarities to closely related species of *Carpinus* which sometimes equal *Quercus* as preferred hosts in Europe (Kurir, 1953; Georgijevic & Vladislav, 1958; Györfi, 1960; Varga, 1969; Marcu, 1972). Similarly, *Amelanchier*, which is a small subcanopy tree never very abundant in the forest (Hosie, 1973), is actually a preferred host of gypsy moth on Lake Hill. Mosher (1915) noted that *Amelanchier canadensis* was a very favourable food plant in his laboratory trials but later workers (Houston & Valentine, 1977) have discounted this early observation. Despite its low abundance and consequent inability to support a large infestation, *Amelanchier* appears to be a preferred host plant for gypsy moth. Finally, *Acer saccharum*, which is a canopy dominant on Lake Hill and in many deciduous forests (Fowells, 1965), has also been reported to be of only intermediate food value and utilized by only a small portion of the gypsy moth population (Mosher, 1915). Preference for such a common but relatively little utilized (compared to *Quercus*, for example) species is difficult to determine from casual field observation. The quantitative analysis presented here shows that *Acer saccharum* was preferentially attacked by

gypsy moth on Lake Hill. Campbell & Sloan (1977a) found conversely that defoliation of *Acer saccharum* in New England forests was very low. This is somewhat surprising since the overall agreement between their reported susceptibility of trees to defoliation by gypsy moth and the Lake Hill feeding preferences is reasonably good (Spearman rank correlation = 0.45; $P=0.10$; $n=15$). *Acer saccharum* near the northern edge of its range in southwestern Quebec may have fewer resources available for allocation to defence and thus may be a more palatable food than it is further south. There are similar regional disparities in the reported preferences for European species of *Acer* (Kurir, 1953; Györfi, 1960; Varga, 1969). Electivity indices provide an effective means to quantify and compare preferences for rare or relatively less utilized host trees whose role in gypsy moth population dynamics has often not been well studied.

Certain genera like *Fraxinus* have long been recognized as avoided by gypsy moth in both North America (Mosher, 1915; Campbell & Sloan, 1977a) and Europe (Kurir, 1953; Györfi, 1960; Varga, 1969; Fratian, 1973). The electivity analysis on Lake Hill affirms the avoidance of *Fraxinus americana* ($E^* = -0.641$) and identifies other species as even more avoided: *Ulmus rubra*, *Acer pensylvanicum*, *A. rubrum*, *Betula lutea* and *Prunus serotina*. With the exception of *A. pensylvanicum*, all of these species fall in Mosher's (1915) intermediate category of not particularly favoured but still utilized foods. This same category includes such preferred hosts on Lake Hill as *Ostrya virginiana* and *Acer saccharum*. Since the polyphagous larvae fed to at least some degree on almost all trees, it is difficult to identify preference and avoidance in this intermediate category based only on laboratory trials and casual field observation. Barbosa's (1978a) quantitative field data also show the avoidance of *Acer rubrum*. Campbell & Sloan (1977a) found all these species to be relatively little used but not as strongly avoided as *Fraxinus* species. The power of the electivity index to discriminate preferred and avoided species within Mosher's intermediate category recommends it in further studies on the feeding preferences of gypsy moth.

This recommendation must be tempered by an awareness of limitations on the inter-

pretation of electivity indices of feeding preferences in leaf-feeding herbivores like the gypsy moth. At least four potential sources of error in estimating feeding preferences exist: (1) under-sampling of rarer tree species, (2) violation of the assumption that host selection had proceeded to some representative equilibrium during dispersal, (3) violation of the assumption that the herbivore population is monotypic, and (4) bias in the measure of host utilization. Each of these problems is briefly considered below.

The dominance–diversity curves of typical deciduous forest communities (Whittaker, 1965) suggest that increasing sample size will not assure that all potential host trees are well represented. Increased sampling will only tend to discover a few individuals of a still rarer species. The calculation of electivity depends on the relative proportions of all potential host trees in the community – the failure to sample a possible host induces an error in all the calculated preferences. This estimation error is, however, inconsequential since the total proportion of such rare species is necessarily small. There is a greater potential error in the estimated preference for the rare species itself. Since it is represented by only a few trees, the rare species is more prone to errors from purely stochastic variation in numbers of larvae feeding on it. If it is necessary to very accurately define feeding preferences for relative rare tree species, quite large sample sizes (on the order of a few thousand trees) will be required to assure a reasonable subsample of each of these rare species. Rare species cannot be selectively sampled since the calculation of electivity depends on an unbiased measure of each tree's relative contribution to canopy composition. Fortunately a not excessively large set of random quadrats sampling about 1000 trees will apparently provide sound estimates of electivity for the majority of the tree species in a deciduous forest.

If the herbivore population has not had equal access to all potential hosts to exercise a preferential choice, then any subsequent calculation of electivity based on feeding counts in relation to host abundance will be biased. Gypsy moth spread by wind-dispersal of first instar larvae – a mechanism which can be limited by weather conditions (Mason &

McManus, 1982). A larvae can move to a new tree, sample its foliage, and either stay or move again. Presumably this behavioural decision reflects preference for the present foliage and the amount of remaining food reserve in the larvae. First instar larvae at hatching have about 3–5 days' food reserve (Forbush & Fernald, 1896). If food reserves are low the larvae may remain on a less preferred host rather than chance further wind-rafting. Dispersal conditions at Lake Hill in 1979 and 1980 suggest that, at the population level, larval distribution in the later instars is representative of feeding preferences. In any later studies of electivity for gypsy moth or other herbivores the possible bias from inadequate dispersal must be considered.

A similar confounding of electivity estimates will occur if the herbivore population is not monotypic, or at least represented by a stable polymorphism. Otherwise the putative feeding preferences of the species will actually represent an amalgam of the narrower preferences in its composite 'host races'. Such host races do not appear to occur frequently in foliage-feeding lepidopterans studied to date (Mitter & Futuyama, 1979; Mitter *et al.*, 1979; Jaenike & Selander, 1980) including the gypsy moth (Roby, 1982). The approach used here to determine gypsy moth feeding preferences will probably be applicable to most tree-feeding herbivores.

Finally, the interpretation of the calculated electivities is ultimately predicated on the method used to census herbivore feeding activity. Sessile trees can be easily tallied but the accurate estimation of herbivores feeding on an individual tree can call for sampling ingenuity and considerable work. If interest centres wholly on preferential food choices by the herbivore, the census needs reflect the life history stage when those choices are made. The problems and limitations of accomplishing this for gypsy moth have been discussed in the methods; similar pragmatic constraints are likely in any study. A census of defoliation levels on individual trees without reference to particular herbivores offers an alternative approach to defining tree susceptibilities to defoliation. Any discussion of preference must remain cognizant of the underlying census techniques lest artefactual results be given full credence.

Even considering these limitations, the feeding preferences determined here for gypsy moth in southwestern Quebec are a useful quantification of earlier observations. The electivity index E^* affirmed early reports of strongly preferred and strongly avoided host tree species. Moreover, the index was able to discriminate preference and avoidance for often abundant trees like sugar maple and ironwood that are less used by the gypsy moth. These have not received adequate attention in the literature and may help elucidate natural tree defences against polyphagous folivores like the gypsy moth. It also seems likely that geographic variation in gypsy moth feeding preferences may exist and affect the continued range expansion of this forest pest. The electivity index E^* offers a sound quantitative basis to describe and compare gypsy moth feeding preferences in diverse habitats. The technique may find similar application in studies of other herbivores feeding on forest trees.

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