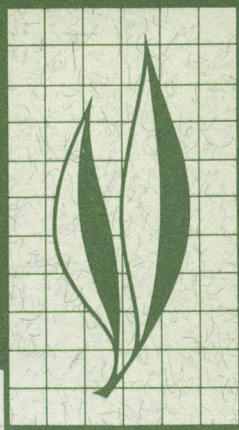


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Ecology of Gall-forming Lepidoptera on *Tetradymia*

I. Gall Size and Shape

II. Plant Stress Effects
on Infestation Intensity

III. Within-plant Horizontal
and Vertical Distribution

Hollister Hartman



I. Gall Size and Shape

Multiway analysis of covariance revealed ecological determinants of gall morphology operating hierarchically, with plant effects primary, insect effects secondary, and habitat effects tertiary. Plant effects included *Tetradymia* DC. (Asteraceae) species identity, timing and duration of growth pulses, and differential vegetation quality among height strata. Insect effects included a numerical response in gall density and a functional response in individual feeding duration and intensity. Alterations in *Gnorimoschema tetradymiella* Busck 1903 (Lepidoptera: Gelechiidae) feeding caused by parasitization created parasitoid-specific gall sizes. Habitat effects indexed by topographic and climatic features operated most strongly in relatively southern latitudes.

II. Plant Stress Effects on Infestation Intensity

Hypothesized differential genotypic galling susceptibility of *Tetradymia stenolepis* Greene 1885 was not confirmed by tests of correlations between sample size and sample variance in plant-mean densities of *Scrobipalpa* n. sp. leaf galls and *Gnorimoschema tetradymiella* Busck 1903 stem galls. An alternate conceptual model, the stress-heterogeneity hypothesis, received support. The greater the stress experienced by a plant subpopulation, the more discontinuous was the frequency distribution of its plant-mean gall abundance. Also according to the model, gall formation increased with stress until a physiological threshold was exceeded, after which it dropped precipitously. Covariance analysis enabled comparisons among plots. Encounter frequency and resource density were also implicated in predicting plant-mean and branch-mean gall densities.

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III. Within-Plant Horizontal and Vertical Distribution

INTRODUCTION

GALL INSECTS DIFFER from most other herbivorous insects in that they must remain in one place, chosen soon after eclosion, until adulthood. In a sense, the outcome of the ecological "game" is completely determined by the player's first "move." The organism's phyletic heritage, like rules written eons in the past, sets the constraints for a life style at once specialist, cryptic, and sessile. Zweigelt (1930 *in* Mani, 1964) argued that gall formation is advantageous for a plant in that it localizes the parasite in time and space, and forces it to extreme specialization.

Explanations for observed distributions of *Gnorimoschema tetradyiella* Busck 1903 and *Scrobipalpa* n. sp. gelechiid moths among *Tetradymia stenolepis* Greene 1885 (Asteraceae) host plants were sought in Hartman (1983b). The horizontal distribution of *Scrobipalpa* n. sp. leaf galls and *G. tetradyiella* stem galls within individual *T. stenolepis* was similarly studied to elicit patterns among plants, elevations, and years. A subsidiary objective was to identify the environmental processes governing these patterns in the New York Mountains, California (for description of study area see Hartman, 1983b).

Vertical distribution was studied to determine the effect of leaf and stem gall densities on gall height. Correlative objectives included finding how *T. stenolepis* foliage distribution and quality were related to each other, and to gall height.

Horizontal distribution: Gall location among quadrants—Agricultural entomologists interested in obtaining accurate infestation estimates often note that insect density varies within a tree according to the cardinal points. Directional insolation, wind, and water flow create differential growth rates and vegetation quality among plant sectors (Friedrick, 1951 *in* Dean, 1959; Ebeling, 1950). Pattern-skewing (also called sector or quad bias) of galls on *Tetradymia* in the New York Mountains was explained as either: 1) Gall insect behavior biasing one or more gall crops toward a particular quad, or 2) gall attrition from animal browse, weather, and shedding of plant parts being least in this quad.

Wind patterns were analyzed to test the former alternative. Moth orientation to host-plant olfactory cues or mating pheromones requires stable, low-velocity breezes to maintain integrity of the aerial trail and/or continuous emission by a pheromone source (Farkas and Shorey, 1972; Kaae and Shorey, 1972; Sower, Kaae, and Shorey, 1973). Gall formation was investigated in terms of new galls being either distributed nearly evenly over the compass points, or concentrated in one or two sectors. Under concentration, the same sector may be chosen every year due to extrinsic environmental influences (termed "bias-clumping," in the sense of a consistent skewing) or the insect may be innately aggregative, but with sectors varying between plants and between years (termed "random-clumping").

Old galls, subject the longest to animal browse, weather, and shedding of plant parts were examined for attrition effects. Three patterns were identified: 1) Loss from a random sector, independent of gall density; 2) loss which was greatest where gall density was highest; and 3) loss which was dispersed evenly over all plant sectors. Animal browse produces

pattern 1, 2, or 3, depending on species of animal and the purpose of its browse. Weather produces pattern 1 or 3, depending on the presence or absence of directionality. Shedding of plant parts, independent of browse or weather, produces pattern 3.

Formation and attrition patterns were combined to produce observed spatial patterns. Common sense excluded some of the nine possible pairings, narrowing alternatives to six:

Mechanism	Observed pattern	Formation pattern	Attrition pattern
1	Uniform	Uniform	Uniform
2	Uniform	Random-clumped	Density-dependent
3	Uniform	Bias-clumped	Density-dependent
4	Random-clumped	Uniform	Random
5	Random-clumped	Random-clumped	Random or Uniform
6	Bias-clumped	Bias-clumped	Random or Uniform

Gall attrition patterns are then deduced from observed patterns and their modes of formation.

Vertical distribution: Gall location among strata—Gall height patterns on *T. stenolepis* varied among insect species, years, elevations, plants, and even among quads on a single plant. Inquiry into the intimate relation between gall height and foliage height distributions made kurtosis, a measure of curve peakedness, an appropriate index of comparison.

Tree growth-potential increases geometrically due to multiple ramifications from trunk to limbs, branches, twigs, and sprouts (Tomlinson, 1983; Honda, Tomlinson, and Fisher, 1982; Strahler, 1957). A plant also possesses an intrinsic growth potential determined by genotypic or microhabitat differences. Slight variations (between soil patches, for example; Hartman, 1977) were thus amplified geometrically in *Tetradymia* crowns. A gallmaker, perceiving a faster foliage drop-off on better-foliated plants, and because rapidly growing productive tissue provided a qualitatively better resource for gall growth and development (Washburn and Cornell, 1981), would tend to remain in a maximum growth stratum. Gallmakers on lower-growth plants were more likely to migrate between strata because of flatter gradients, leading to “spread” distributions with negative kurtoses.

The above strata-gradient model scenario was tested to account for the greater vertical concentration of leaf galls on fully-foliated *T. stenolepis*. Alternative mechanisms for observed patterns were:

Case 1) Gallmakers are initially unbiased as to vertical stratum but with density increases their distribution corresponds more closely to the foliage distribution; or

Case 2) Gallmakers are initially biased toward a particular vertical stratum but as density increases they are “crowded” into less-preferred strata.

Support for the assumption of steeper gradients among vigorous plants would include showing that as some measure of vigor increased (e.g., density of leaf budding, shoot production, or flowering; cf. Nilsen and Muller, 1981), the spatial concentration of this measure also increased.

METHODS

Horizontal distribution—Four sectors (NE, NW, SW, SE) were delimited for each host plant by sighting with a magnetic compass. Analysis of covariance allowed one-way ANOVA's of inter-sector gall densities to be interpreted as though all were based on the same-sized plants at plots with the same degrees of infestation.

Wind direction and an index of relative speed were recorded morning, noon, afternoon, and evening, April 1978 to September 1979. Anemometer measurements indicated that recorded scores of one, two, or three corresponded to ca. 1.4 to 4.3 mph, 3.8 to 8.5 mph with gusts to 10 mph, and 5.5 to 13.5 mph with gusts to 16 mph, respectively. Areas of overlap in the above speed ranges were assigned scores according to whether wind speed fluctuated above or below marginal values. A rough index of breezes suitable for insect aerial trail-following was formed by taking the ratio between direction-specific wind frequencies and their magnitudes, to maximize wind stability and minimize velocity.

Interquad gall distribution was enumerated for 40 *T. stenolepis* in April 1977 and 48 in April-May 1978. One-sample chi-square tests assessed deviation from uniformity among quads, for each plant. Contingency tables tested the independence of different elevations and gall-age classes.

Moderately-infested plants were studied to determine if gall distribution was uniform or clumped. Clumping was best detected at "moderate" gall densities per plant because at very low densities numbers were so few that biases went undetected; at very high densities, crowding forced spreading to all sectors. Infestations at 1122 m were thus most likely to exhibit clumping, if it existed, in the New York Mountains. Random- and bias-clumping were distinguished by comparing distributions among plants. The same sector favored on all plants indicated the latter alternative. Accordingly each plant with at least 20 new stem galls (to provide a minimum expected frequency of five per cell) was subjected to a chi-square test.

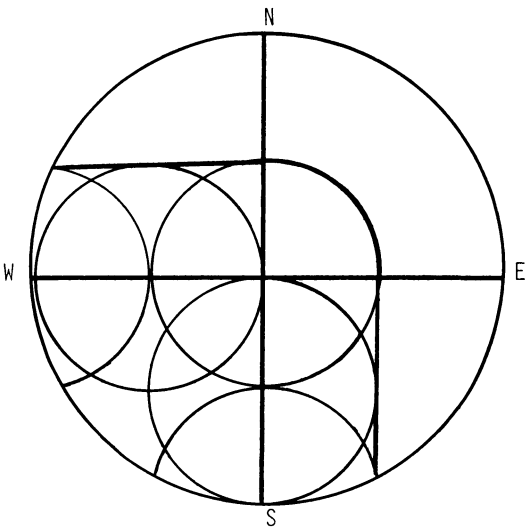


Fig. III.1. Maximum dispersal distances of gall larvae from inner southwest quad margins, assuming individual distances not exceeding half the plant radius.

Quad	Geometric approximation	Area	Percent of area
NE	quarter circle	$\pi(0.5r)^2/4 = .196r^2$	.100
NW	rectangle	$r(0.5r) = .500r^2$	.252
SE	rectangle	$r(0.5r) = .500r^2$	.252
SW	quarter circle	$\pi(r)^2/4 = .785r^2$	.396
			1.000

The deviant proportions of new leaf galls in 1977 (see Results) prompted the question of whether their SW quad bias was consistent among all plants, or shown on only a few heavily-infested plants. As a basis of comparison I quantified the normative SE bias among new leaf galls in 1978, then repeated a similar analysis on 1977 data for the SW quad. To test a random-diffusion explanation of the SW quad bias, theoretical quad-mean abundances were derived from relative areas covered by diffusion (e.g., Fig. III.1). Analogous computations assumed a range of values for maximum diffusion distances.

Vertical distribution—Correlations between number of new leaf galls per quad and their quad-mean height, for each of the 48 plants sampled in the New York Mountains, 1978, were averaged within elevations using Fisher's (1921) Z transformation. New stem galls from 1978, old stem galls from 1977, and old stem galls from 1978, were analyzed separately. Groups with correlations of the same sign were combined and new coefficients computed to find if the relationship persisted for the pooled sample.

I verified the strata-gradient model assumption of a positive association between plant vigor and spatially-concentrated tissue quality by quantifying *Tetradymia* shoot production via the method of Steingraeber, Kascht, and Franck, (1979). A mean of 8.4 branches per plant (mean maximum basal diameter 3.7 to 6.4 mm) was removed from each of ten specimens in the New York Mountains at 1122 m and 1138 m, 18 February to 28 April 1979 (a major growth period of Mojave Desert shrubs). The lengths of all twigs and sprouts from each branch were recorded in a histogram with 5-cm intervals. Density of shoot production was computed as number of sprouts per twig for each plant.

Number of sprouts per length category (0-5, -10, -15, -20 cm) was converted to percentages; the greater the population standard deviation over these four categories for each plant, the more localized was shoot production. The strata-gradient model required that as number of sprouts per twig increased, this standard deviation increased.

Gall heights were divided by plant height to create a vertical stratification index comparable among all *T. stenolepis*. Kurtosis of these "relative heights" for each plant was computed separately for leaf and stem galls. New stem galls, not recorded in 1977, were approximated with old stem galls sampled in 1978. Kurtosis was then plotted as a function of the number of each gall type on the plant. Moving averages calculated for two- to five-point intervals of the domain served as a curve-smoothing method.

RESULTS

Horizontal distribution—Because F values were nonsignificant for gall density per rank in quad sampling sequence (Hartman, 1982a, b), sampling order did not affect gall counts per quad. Distribution of each gall type (new leaf, old leaf, new stem, old stem) among plant sectors is given in Table III.1.

The strongest and most numerous winds came out of the west, with the opposite holding true for the east (Table III.2). North and south winds were of intermediate frequency, with south winds averaging ca. 11.8 percent stronger than north winds. Cumulative totals led to expectations of NW and SW winds being 69.3 percent more frequent than those out of the NE or SE, and 33.3 percent stronger. Times of day for the strongest winds were noon and afternoon, with mean relative magnitudes ranging from slight breezes to moderate winds.

Stable, low-velocity winds suitable for aerial trail-following emanated mainly from the east and north (Table III.3). When the sum of all index ratios for breezes in the early

TABLE III.1 FREQUENCY DISTRIBUTION OF GALLS AMONG COMPASS QUADRANTS OF *T. STENOLEPIS* IN THE NEW YORK MOUNTAINS, APRIL 1977 TO APRIL 1978

Year	Elevation	Gall type	Percent each quad				Number galls	Chi square
			NE	NW	SW	SE		
1977	1122 m (n = 12)	Leaf (new)	.303	.227	.227	.243	317	4.931 (p = .177)
		(old)	.233	.167	.300	.300	180	8.800 (p = .032)
		Stem	.125	.375	0	.500	8	1.750 (p = .417)
		Web*	.172	.448	.138	.241	29	6.724 (p = .081)
	1138 (n = 15)	Leaf (new)	.160	.210	.320	.309	181	13.144 (p = .004)
		(old)	.259	.237	.232	.272	224	0.964 (p = .810)
		Stem	.118	.235	.353	.294	17	2.059 (p = .560)
		Web*	.222	.352	.222	.204	108	6.074 (p = .108)
	1268 (n = 13)	Leaf (new)	.223	.204	.320	.252	103	3.214 (p = .360)
		(old)	.316	.160	.228	.296	399	23.827 (p = 0)
		Stem	.289	.211	.211	.289	38	0.947 (p = .814)
		Web*	.222	.667	.111	0	9	4.667 (p = .097)
	1122 m (n = 16)	Leaf (new)	.223	.179	.251	.346	358	22.326 (p = 0)
		(old)	.265	.259	.239	.237	929	2.000 (p = .572)
		Stem (new)	.217	.243	.243	.297	515	6.965 (p = .073)
		(old)	.221	.224	.180	.374	294	25.592 (p = 0)
	1138 (n = 16)	Leaf (new)	.294	.194	.211	.300	180	6.533 (p = .088)
		(old)	.277	.178	.275	.270	426	11.690 (p = .009)
		Stem (new)	.270	.243	.297	.189	37	0.946 (p = .814)
		(old)	.338	.212	.225	.225	80	3.300 (p = .348)
	1268 (n = 16)	Leaf (new)	.255	.188	.248	.309	165	4.867 (p = .182)
		(old)	.240	.216	.236	.308	292	5.671 (p = .129)
		Stem (new)	.258	.219	.289	.234	128	1.438 (p = .697)
		(old)	.182	.206	.273	.339	165	9.958 (p = .019)

*Unidentified Gelechioidea

morning (the main activity period of the gall-forming moths) was subdivided according to compass direction, the proportion contributed was greatest for the NE, at 34.5 percent, and least for the SW, at 17.1 percent. Thus the directional distribution of frequent light winds was consistent with SW-biased leaf gall moth oviposition.

New leaf gall frequency distributions sampled in April 1977 were roughly the same at all three elevations studied (1122 m, 1138 m, 1268 m). Pooled proportions (19.4% NE, 20.7% NW, 32.0% SW, and 27.9% SE) showed a significant bias toward the south (chi-square(1) = 15.320, $p < .001$). Old leaf galls were distributed significantly differently

TABLE III.2 SUMMARY STATISTICS FOR DAILY CHANGES IN WIND DIRECTION AND RELATIVE MAGNITUDE IN THE NEW YORK MOUNTAINS, 1978 TO 1979

Time of day:	Relative magnitude*							
	0700-0800		1100-1300		1500-1600		1900-2000	
Wind direction†	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
North	0.559 (n = 34)	0.705	1.414 (n = 35)	0.772	1.550 (n = 20)	0.887	0.565 (n = 23)	0.945
South	0.829 (n = 35)	1.071	1.720 (n = 25)	1.011	1.540 (n = 25)	1.020	0.774 (n = 31)	0.884
West	0.872 (n = 47)	0.900	1.629 (n = 58)	0.781	1.674 (n = 43)	0.830	0.861 (n = 36)	0.867
East	0.304 (n = 23)	0.765	1.222 (n = 9)	1.093	1.083 (n = 12)	1.084	0.333 (n = 18)	0.840

*1 = faint breeze, 2 = strong breeze to moderate wind, 3 = strong wind

†	Wind direction	Mean magnitude	Relative frequency
	North	1.005	.236
	South	1.160	.245
	West	1.296	.388
	East	0.597	.131
			1.0

TABLE III.3 INDEX OF BREEZES SUITABLE FOR AERIAL TRAIL-FOLLOWING BASED ON SUMMARY STATISTICS FOR DAILY CHANGES IN WIND DIRECTION AND RELATIVE MAGNITUDE IN THE NEW YORK MOUNTAINS, 1978 TO 1979

Wind direction	Time of day:	Index = $\frac{\text{Wind frequency}}{\text{relative magnitude}}$			
		0700-0800*	1100-1300	1500-1600	1900-2000*
North		60.82	24.75	12.90	40.71
South		42.22	14.53	16.23	40.05
West		53.90	35.60	25.69	41.81
East		75.66	7.36	11.08	54.05
	Mean =	58.15	20.56	16.48	44.16
	S.D. =	13.971	12.307	6.503	6.638

*Suitability for aerial trail-following significantly exceeds other times of day. During this period suitable winds predominate from the north and east.

from new leaf galls, both at each elevation and over all elevations pooled (chi-square(3) = 14.276, $p < .01$ for the pooled case). Old leaf gall proportions of 28.1% NE, 18.3% NW, 24.5% SW, and 29.0% SE showed an east- rather than south-bias.

Leaf galls sampled in April 1978 differed from those of 1977 in that new and old gall distributions among quads were statistically indistinguishable (except at 1122 m, where old leaf gall counts were significantly more uniform). Patterns of leaf galls at 1138 and 1268 m did not differ (chi-square(3) = 3.064, $p = .3-.5$); these, pooled, did not differ from new leaf galls at 1122 m (chi-square(3) = 5.890, $p = .1-.2$).

Stem gall distribution was more consistent between years and elevations than that of leaf galls. Fuzzy old stem galls collected in April 1977 (i.e., those formed in 1976) were uniformly distributed and hence unbiased with respect to quad preference, both for each elevation and over all elevations pooled (chi-square(3) = 0.429, $p = .934$). New stem galls counted in 1978 were similarly unbiased with respect to quad preference (chi-square(3) = 4.970, $p = .180$). Old stem galls at 1138 m were included since they too were uniformly distributed.

Old stem galls at 1122 and 1268 m, however, shared a common distribution (chi-square(3) = 5.595, $p = .1-.2$) which differed significantly from uniformity (chi-square(3) = 30.630, $p < .001$). Their proportions of 20.7% NE, 21.8% NW, 21.4% SW, and 36.2% SE deviated markedly toward the SE. In summary, at least two stem gall crops (1976 and 1978) showed no quad preference, yet accumulations of older crops were biased.

Results of 11 chi-square tests on plants with at least 20 new stem galls (Methods) showed seven plants with uniformly-dispersed galls and four plants with randomly-varying sector biases. This implied that stem gall insects spread themselves evenly throughout the plant (cf. Hartman, 1983b, Fig. II.4).

Old leaf galls sampled in 1977 and total leaf galls from 1978 (except old at 1122 m, explained above) were similarly proportioned among quads (chi-square(3) = 2.215, $p = .5-.7$). Counts pooled over elevations (26.3% NE, 18.6% NW, 25.3% SW, and 29.8% SE) are henceforth defined to be normative proportions. New leaf galls sampled in 1977 deviated substantially from these proportions, with a positive SW bias.

The above bias toward the SE quad was characterized as follows: 1) 42 percent of all plants had too few new leaf galls for chi-square analysis; 2) Of the plants included, 43 percent had no quad bias; 3) Of the plants with a bias, 47 percent showed a SE bias;

TABLE III.4 FREQUENCY DISTRIBUTIONS AMONG COMPASS QUADRANTS, OF LEAF GALLS ON *TETRADYMIA*, PREDICTED BY RANDOM DIFFUSIONS FROM THE SOUTHWEST QUADRANT OF A PLANT WITH RADIUS R

Maximum diffusion distance	Quad:	Expected quad-mean number of leaf galls resulting from given diffusion distance*			
		NE	NW	SW	SE
0		0	0	284.0	0
.25 r		15.1	30.9	207.0	30.9
.50 r		28.1	71.6	112.5	71.6
.75 r†		49.4	73.4	87.8	73.4
r		71.0	71.0	71.0	71.0

*Based on observed total of 284 new leaf galls at 1138 to 1268 m, the New York Mountains, 1977. Frequencies computed from geometric approximations of relative areas.

†Expected frequencies not significantly different from observed frequencies of 52, 59, 91, 82.

$X^2(3) = 4.0862$, $p = .253$

4) The SE quad was ranked from first to second in number of new leaf galls by 68 percent of all plants; 5) Plants whose SE quad was ranked first to second bore a mean of four more new leaf galls than those ranked third to fourth.

Leaf galls from 1977, although centered around the SW quad rather than the SE, had similar distribution characteristics: 1) 50 percent of plants had too few new leaf galls for chi-square analysis; 2) Of the plants included, 43 percent had no quad bias; 3) Of the plants with a bias, 38% showed a SW bias; 4) The SW quad was ranked first to second by 61 percent of all plants; 5) Plants whose SW quad was ranked first to second averaged 8.9 more leaf galls than those ranked third to fourth ($t(29) = 1.757, p = .092$).

Artificially-generated larval mobility patterns preceding gall initiation (Table III.4) revealed that strictly random movement from the SW quad, not exceeding 75 percent of the plant's radius, produced frequencies actually observed for leaf galls at 1138 to 1268 m in 1977 (pooled goodness-of-fit chi-square(3) = 4.086, $p = .253$). This implied limited, random leaf-gallmaker dispersal to adjacent sectors following primary occupancy of the SW quad.

Vertical distribution—Correlations between galls per quad and quad-mean gall height above the ground were pooled over 1977 and 1978 (data given in Hartman, 1983a, Table I.5). Pearson coefficients were generally better for new than old galls, with $r(22) = .636$ ($p = 0$) for new leaf galls, $r(22) = .140$ ($p = .257$) for old leaf galls, $r(10) = .683$ ($p = .007$) for new stem galls (1978 only), and $r(22) = .244$ ($p = .131$) for old stem galls.

Calculating the new leaf gall density-height correlation for each plant in 1978, rather than over all plants, yielded Fisher's-mean correlations of $-.418$ (60.0% of plants negative) at 1122 m, $-.360$ (38.5% of plants negative) at 1138 m, and $+.192$ (27.3% of plants negative) at 1268 m. The overall negativity implied that contrary to the above among-sites relation, the greater the new leaf gall density, the *lower* the gall height.

Comparing mean new leaf-gall heights among *T. stenolepis* falling in three foliage categories showed that mean kurtosis within the first category (upper half and outer shell) was $-.285$ while within the last category (entire height and entire volume), it equaled $+.984$ ($t = 2.0544, p = .05$). Also, 71.4 percent of the plants with entire foliage had positive kurtosis, compared to only 38.9 percent of those lacking either lower or inner foliage (chi-square = 3.342, $p = .05-.10$). Thus leaf galls sampled in April 1978 were distributed more evenly than host plant foliage.

TABLE III.5 SUMMARY STATISTICS FOR PLANT-MEAN RELATIVE GALL HEIGHT KURTOSIS OF *T. STENOLEPIS* IN THE NEW YORK MOUNTAINS, 1977 TO 1978

Gall type	Sign of kurtosis:	Percent of plants		Mean kurtosis		Galls per plant		Number of plants*
		+	-	+	-	+	-	
Leaf								
(new)	1977	.345	.655	0.992	1.001	26.20	16.84	29
	1978	.512	.488	1.499	0.953	17.24	16.55	41
(old)†		.383	.617	1.078	0.817	39.89	31.93	47
Stem								
(new)†		.364	.636	1.549	0.803	11.33	24.81	33
(old)†		.412	.588	1.361	1.085	13.36	16.65	34

*Includes only those plants with ≥ 4 galls, for purposes of kurtosis computation.

†1978 only

About twice as many plants in 1977 had negatively kurtotic gall height distributions as positive; degree of deviation from normality was the same for each sign (+.992 for peaked curves and -1.001 for flat curves) (Table III.5). Plants with peaked distributions, however, had significantly more galls than those with flat curves ($t = 1.888$, one-tail $p = .02-.05$). Thus, vertical concentration occurred on two levels: more galls on fewer plants, and more galls in fewer strata within each plant.

The positive association between sprout production and statistical variance in sprout length demanded by the strata-gradient model was confirmed:

$$\log y = 0.3133x + 0.8898 \text{ (} r(8) = .851, p = 0 \text{)}.$$

In applying the model, expected paraboloid shapes emerged (a positive U-curve for Case 1, and a negative inverted-U for Case 2; Introduction) (Fig. III.2a, b, c). All gall types conformed to Case 2, for both years, at 1138 m. The remaining cases conformed to Case 1, with the exception of new leaf galls at elevations 1122 m and 1268 m in 1978.

DISCUSSION

Horizontal distribution—Leaf galls formed by *Scrobipalpa* n. sp. on *T. stenolepis* were statistically skewed more often than stem galls formed by *G. tetradymiella*. Given a randomly-expected gall distribution of 25 percent per quad, new and old leaf gall dispersions usually agreed in exceeding the expected value in the SE quad and falling short in the NW quad. This skewness was tied to the 4 percent NW-facing slope of Prospect Canyon in the New York Mountains. Old leaf galls sampled in 1978 at 1122 m, however, were unexpectedly uniformly-dispersed among plant sectors. New leaf galls sampled in 1977 were unusually

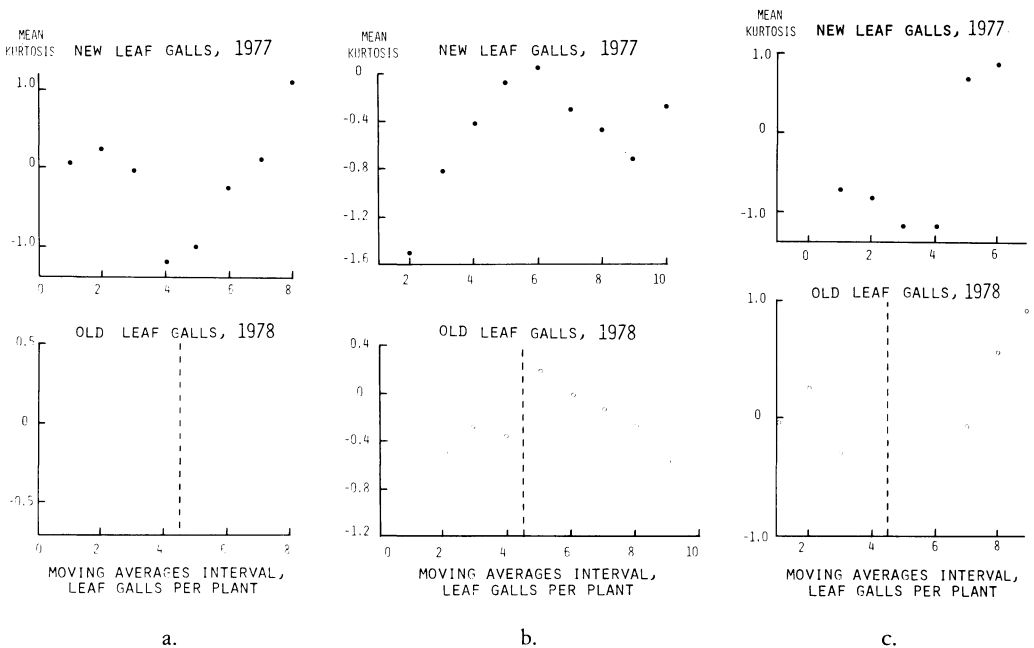


Fig. III.2. The relationship between numbers of leaf galls per plant and the mean kurtosis of their vertical height distribution in the New York Mountains, 1977 versus 1978. a. Elevation 1122 m; b. Elevation 1138 m; c. Elevation 1268 m.

concentrated in the SW and greatly reduced in the NE, compared to leaf gall crops of other years.

According to Mechanism 3 of the attrition model (Introduction), the uniform leaf gall distribution in 1978 would be due to the NW quad suffering the lightest loss and the SE quad, the heaviest. Such attrition raised the relative density of NW galls (normatively the sparsest) to the mean level, and lowered the SE gall density (normatively the densest) to the mean level. The gall attrition mechanism was thus density dependence.

The consumption of clumped galls exceeding that of isolated galls is analogous to observed browse of clumped *T. stenolepis* in the New York Mountains exceeding that of isolated plants. The former may have occurred in 1977 if rodents at 1122 m consumed *Scrobipalpa* leaf galls (containing late instars) for moisture and protein. Felt (1940) also noted that "some of the smaller, warm-blooded animals prey upon the larvae of gall insects and in certain cases obtain a very acceptable addition to their more usual fare." Davis (1931) found many galls produced by *Gnorimoschema gallaesolidaginis* which had evidently been eaten into by a mouse.

Analysis of wind patterns suggested that aerial trail-following leaf gall moths would first encounter the SW sector of each plant. Calculations showed the observed distribution of galls among sectors to be consistent with random diffusion from this quad, with mean dispersal distance not exceeding 75 percent of the plant's radius. Conditions absent in 1977, such as heavy winter rains, may facilitate SE-ward larval migration in other years (cf. Hartman, 1982a, Appendix 25).

The even distribution of new stem galls among quads was contrasted with the old stem gall bias toward the SE. To find whether old stem galls sampled in 1978 were skewed because of differential formation, or differential attrition, I examined causes of the *new* gall equal distribution among sectors. Alternatives included spatial uniformity due to: 1) extremely light or heavy *G. tetradymiella* infestations, masking true concentration; 2) the summation over many randomly-clumped sectors; or 3) a true behavioral uniformity.

Goodness-of-fit chi-square tests applied to new stem gall distributions on individual host plants favored alternative three. Assuming consistent *G. tetradymiella* gall-formation behavior each year, the SE-bias of old stem galls was, therefore, probably absent at the time of gall formation. In terms of the attrition model (Introduction), a composite mechanism by which galls in the SE quad suffer the fewest losses at 1122 m and 1268 m and losses equal to those of the other quads at 1138 m is required.

Vertical distribution—Two trends dominated the association between *Scrobipalpa* leaf gall density and height in 1978: 1) When all host plants at a site were compared with those at another site, denser sites had higher galls; and 2) when quad heights were compared within plants, denser quads often had lower galls. The latter case might be explained by the distribution of leaf galls expanding vertically with increasing quad occupation. Independently-collected data from 1977 were examined to test the likelihood of this phenomenon, as follows.

The correlation between number of new leaf galls per quad and quad-mean gall height variance was calculated for each host plant sampled in April 1977. Of 31 coefficients, 25 were positive; elevation-mean correlations ranged from +.600 to +.805. This confirmed that if only a few galls occupied a plant sector they were likely to share the same vertical stratum, but as more galls were added, more strata were utilized.

For stem galls, the consistency of the relationship between denser galls and greater quad-mean heights over all elevations, years, and gall ages emphasized its probable biological importance. Because a sprout subsumes a substantial part of *Tetradymia* height, making theories involving foliage distribution inapplicable, bifurcation ratios (which index degree

of branching) were instead examined. Although the ratios are traditionally considered to be species-specific, Steingraeber et al., (1979) found significant differences between sugar maples growing in open versus shady patches. They attributed this to adaptive phenological plasticity.

About half of *T. stenolepis* in the New York Mountains were similarly observed to have higher bifurcation ratios than others, which I termed "stemmers" and "branchers," respectively. Brancher sprouts originated mainly from the upper half of the plant, while stemmer sprouts originated from the lower limbs. This mandated that branchers have many short sprouts and stemmers have fewer long sprouts, possibly accounting for the observed density-height correlation.

Case 1 and Case 2 of the strata-gradient model (Introduction) were distinguished by examining *Scrobipalpa* leaf gall height versus gall density. In Case 1, the peakedness of the distribution initially decreased (more galls—more strata occupied), then increased (high-capacity strata contain more galls than low-capacity strata). In Case 2, the peakedness of the distribution initially increased (more galls—concentration in preferred stratum), then decreased (movement into less-preferred strata).

The exceptional rate of *T. stenolepis* establishment and growth at 1138 m, far exceeding that at other elevations, indicated conditions promoting optimal *Tetradymia* growth. Thus, as posited by the strata-gradient paradigm, galls were most vertically concentrated on the most vigorous plants. Because new leaf galls sampled at 1122 m and 1268 m in 1978 also conformed to Case 2, all leaf galls sampled in 1978 occurred at heights expected from growth at 1138 m. Heavy winter rains, which would greatly increase soil moisture reserves compared to sporadic summer downpours (Shreve, 1914), distinguished 1978 from the preceding several years. Hence *T. stenolepis* host plants at 1138 m in 1978 may have lost their advantage over those at other elevations, in terms of the vigor sensed by *Scrobipalpa* and *G. tetradymiella*.

To test the above explanation against the alternative that new leaf gall heights in 1978 were simply anomalous, old leaf gall data sampled in 1978 were examined. The data were expected to exhibit a Case 1 pattern, similar to that of 1977 new leaf galls, both because old leaf galls: 1) partially derived from the previous year's crop; and 2) had not been exposed to unusually heavy winter rainfall. Kurtosis plotted as a function of gall density (Fig. III.2a, b, c) significantly paralleled analogous plots of new leaf galls from 1977. At 1138 m *Tetradymia* showed pattern two, evidently due to growing in vigor-inducing conditions; when these conditions became more widespread, so did the second pattern.

Resource-limitation of gall sites in strata of maximum *Tetradymia* growth was inferred. Scriber and Feeny (1979) found a general association between leaf water content and caterpillar growth rate, which they related to leaf variation in nitrogen content, toughness, and fiber content. Gall insects may be "forced" into adjacent, less-optimal strata, with optimality construed as leaf growth rate. Faster leaf growth provides more, higher-quality food for the encased larvae, which grow faster and larger, and are thus able to leave the gall for pupation sooner (avoiding chances of predation, ultimately producing more eggs as an adult). Intraspecific spatial competition among adults can also restrict population growth. Faeth (1980), for example, recognized possible resource limitation of oak-mining gracillariids from the preferential oviposition by female moths on unshaded leaves.

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