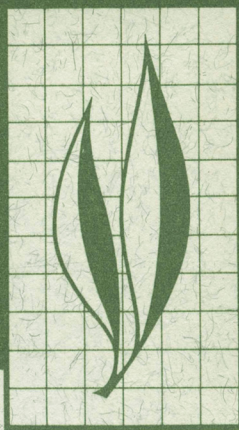


HILGARDIA

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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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II. Plant Stress Effects on Infestation Intensity

INTRODUCTION

ALTHOUGH ONLY 100 species of gall-forming Lepidoptera were recorded worldwide by Mani (1964), they are probably more numerous and ecologically important than usually recognized. Gall moths have received little attention in North America, with the possible exception of *Gnorimoschema gallaesolidaginis* Riley on *Solidago* (e.g., Barber, 1938; Beck, 1953; Blum, 1952; Cosens, 1910; Hartnett and Abrahamson, 1979; Judd, 1967; Leiby, 1922; Mills, 1969; Stinner and Abrahamson, 1979).

In Hartman (1983a), ecological factors controlling the morphology of galls made by the gelechiid moths *Gnorimoschema tetradytiella* Busck 1903 and *Scrobipalpa* n. sp. on *Tetradymia* DC. (Asteraceae) were investigated. The host plant *T. stenolepis* Greene 1885 is a low, rigid shrub covered with dense white wool and bearing yellow flowers. The leaves are often modified into spines. It is variously called horsebush (Thorne, Prigge, and Henrickson, 1981), horsebrush (McMinn, 1951) or felt-thorn (Jaeger, 1969).

Gall moth infestations on *T. stenolepis* were notable for their discontinuities. Of two adjacent plants matched for size and condition, one might remain untouched while the other was heavily gall-infested. Felt (1940) also noted that gall formation is "ordinarily restricted to an individual tree or a group of trees."

Explanations for such variability include individual plants within a population having genetic resistance or susceptibility to herbivorous insect attack (e.g., Edmunds and Alstad, 1978; Hanover, 1975; Jones, 1973). Alternatively, host plants may develop resistance in response to heavy attack (Haukioja, 1980; Washburn and Cornell, 1981). Selective breeding by agricultural researchers may not, however, yield resistant offspring (e.g., Tingey and Singh, 1980; Ellis and Eckenrode, 1979). Lack of heritability is associated with either invariant traits essential to the fitness of an organism, or variation which is purely environmental (Falconer, 1960).

Feeny (1976) instead attributed much intraspecific variation in resistance levels to differences in "apparency" caused by clump size, microhabitat, growth form, neighboring plants, population density and number, pathogens, and herbivore host-finding adaptations. The following alternatives were tested for *T. stenolepis* galls:

H(o): The variability in number of galls per plant is entirely accounted for by environmental factors such as plant density, animal browse, rainfall, etc.

H(a): Even after environmental differences are held constant, significant residual variability in number of galls per plant remains, pointing to the possibility of genotypic differences.

A stress-heterogeneity hypothesis was formulated as a testable alternative explanation for all-or-nothing gall infestation. Formally stated, the hypothesis holds that the greater the stress on a subpopulation of plants, the more discontinuous will be the frequency distribution of plant-mean gall abundances (Fig. II.1). Noy-Meir (1973) cited similarly increased year-to-year variations in litter fall as mean annual rainfall decreased. Outbreaks of diverse phytophagous insects have been correlated with appropriate stress indices (Wearing and van Emden, 1967; Wearing, 1967; White, 1969).

My primary objective was to explain *Scrobipalpa* n. sp. leaf gall and *G. tetradytiella* stem gall spatial distributions among *T. stenolepis* host plants. Correlative objectives were to test for the presence of a heritable predisposition toward gall formation, to formulate a theoretical gall distribution model, and to link characteristics of the plant and its environment with leaf and stem gall abundances.

METHODS

Three elevations were studied in Prospect Canyon of the New York Mountains in the eastern Mojave Desert, 6.4 km south of Ivanpah, San Bernardino County, California (Fig. II.2). Dominant perennials other than *T. stenolepis* included *Yucca schidigera* Roehl ex Ortgies, *Coleogyne ramosissima* Torr., *Larrea tridentata* (Sesse and Moc. ex DC) and *Hilaria rigida* (Thurb.) Benth. ex Scribn. Leaf litter was typically absent above elevation 1127 m and the *Tetradytiella* were smaller and more numerous than at other southern California localities (see also Hartman, 1982a).

To test the hypothesis of genetically determined gall susceptibility, I quantified the variance increase that tends to accompany sample size decreases (due to the proportionately greater contribution of each tail point). If variance in gall density of a plant population successively divided into categories homogeneous with respect to environmental factors decreased, then the subdivision (and hence the corresponding environmental factors) explained gall distribution among plants without invoking differential gall resistance.

Many environmental factors may have no effect on partitioning variation in gall abundance (i.e., are unsuccessful variables), but any set of independent variables producing a significantly positive slope for the regression of variance as a function of sample size (n) requires acceptance of the null hypothesis.¹ The first division made was by elevation (1122, 1138, 1268 m), followed by subdivision above and below the median *T. stenolepis* height. Remaining environmental variables (Fig. II.3; see also Hartman, 1982a, Appendix 8) were used in turn as third subdivisions, and the resulting (sample size, variance) correlations calculated.

If the stress-heterogeneity hypothesis (Fig. II.1) were correct, I expected to observe the following:

- 1) On lightly-stressed plants (left of line A), gall density is well-predicted by monotonic variation in stress levels. On heavily-stressed plants (right of line A), gall density is not a first-degree function of stress levels.
- 2) Lightly-stressed plants show less variability in gall density than heavily-stressed plants.
- 3) At less-than-extreme levels of stress (left of line B), gall density increases as stress increases.

Testing criterion one made reference to the results of the preceding tests for genetic resistance. The *T. stenolepis* host plants at each elevation were rated on the frequency of

1. Conditions ensuring valid test results include:

- (1) Refraining from statistically controlling independent variables which themselves may be correlated with genotypic variability in gall susceptibility. Variables characteristic of the plants *per se* with no possible relation to external conditions were eliminated.
- (2) Confirming the existence of at least some heavily-infested *Tetradytiella*. Folivorous insects are often rare relative to their food supplies (Lawton and Strong, 1981). During an overall low-level year no distinction can be made between plants with few galls for genetic reasons versus external reasons. The test was conducted during "outbreak" years or confined to patches supporting some heavily gall-infested plants.
- (3) Checking that the distribution of values being partitioned (number of galls per plant) was symmetric. Square root transformations were applied.

the following stress indicators: missing foliage, interspecific plant contact, atypical leaf size and density, poor sprouting, heavy animal browse, and sprawling or asymmetric growth forms. A negative association was expected between the success of each host plant feature in predicting gall density and the stress indicated by that feature.

Although many factors are involved in determining plant density, such as seed dispersal, germination, establishment of young plants, and continued survival in the face of hostile physical and biotic parameters, ultimately sparse populations occupy more stressful habitats

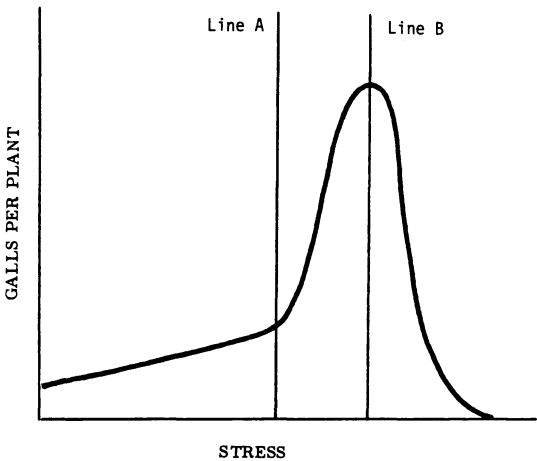


Fig. II.1. Stress-heterogeneity model: Each locality imposes an overall stress on *Tetradymia*, while each plant experiences more or less than this level depending on microhabitat differences. According to this model, a low-stress site would place most plants to the left of line A while a high-stress site would place most plants to the right. Up to a point, the greater the stress on the plants, the more heavily galled they are expected to be. At extreme levels of stress, however, (to the right of line B) the physiological functioning of the plant would be impaired (including the ability to form galls).

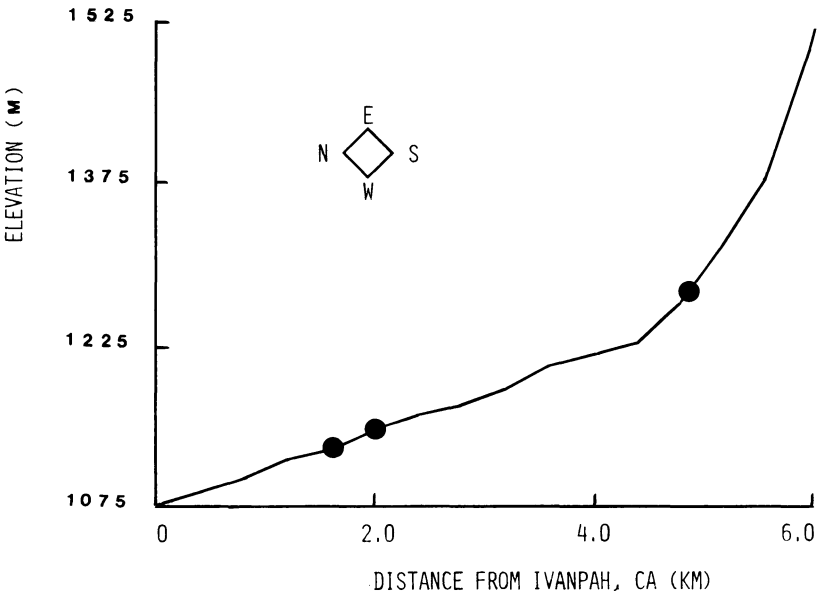


Fig. II.2. Location and elevation of study plots in the New York Mountains, California.

	Date:
	Plot:
	Subplot:
	Neighbor distance:
Wash within 10 m?	
Road within 10 m?	
Subcanopy grasses or annuals?	
Contact with small shrub?	
Proximity with large shrub or tree?	
Animal browse?	Heavy <input type="checkbox"/> Light <input type="checkbox"/> None <input type="checkbox"/>
Animal burrow?	
External insects?	Heavy <input type="checkbox"/> Light <input type="checkbox"/> None <input type="checkbox"/>
Soil insects?	
Litter?	Heavy <input type="checkbox"/> Light <input type="checkbox"/> None <input type="checkbox"/>
Dead branches?	Understory <input type="checkbox"/> Section <input type="checkbox"/> Interspersed <input type="checkbox"/>
Plant shape?	Robust <input type="checkbox"/> Average <input type="checkbox"/> Scrawny <input type="checkbox"/>
	Tight <input type="checkbox"/> Average <input type="checkbox"/> Loose <input type="checkbox"/>
	Symmetric <input type="checkbox"/> Bad branch <input type="checkbox"/> Asymmetric <input type="checkbox"/>
Foliage?	Dense <input type="checkbox"/> Average <input type="checkbox"/> Scanty <input type="checkbox"/>
Foliage distribution?	Entire height <input type="checkbox"/> Upper only <input type="checkbox"/>
	Entire volume <input type="checkbox"/> Outer only <input type="checkbox"/>
Leaf size?	Small <input type="checkbox"/> Average <input type="checkbox"/> Large <input type="checkbox"/>
Spines?	Gray <input type="checkbox"/> Brown <input type="checkbox"/>
	Long <input type="checkbox"/> Short <input type="checkbox"/>
	Robust <input type="checkbox"/> Thin <input type="checkbox"/>
Sprouts?	Copious <input type="checkbox"/> Fair <input type="checkbox"/> Some <input type="checkbox"/> None <input type="checkbox"/>
	Length =
Flowers?	Copious <input type="checkbox"/> Fair <input type="checkbox"/> Some <input type="checkbox"/> None <input type="checkbox"/>
	Closed <input type="checkbox"/> Partially open <input type="checkbox"/> Fully open <input type="checkbox"/> Dry <input type="checkbox"/>
General condition?	Outstanding <input type="checkbox"/> Excellent <input type="checkbox"/> Good <input type="checkbox"/>
	Fair <input type="checkbox"/> Poor <input type="checkbox"/> Critical <input type="checkbox"/>
Comments:	

Fig. II.3. Sample data sheet for *T. stenolepis* host plant features in the New York Mountains.

than dense ones (e.g., Ferguson, 1964). Also the less stressful the site, the greater was expected to be the proportion of actively growing young plants. Hence, an index of relative stress was computed by dividing the percent of mature (vegetation volume exceeding 42 cu dm per plant) *T. stenolepis* at each of six elevations sampled in September 1977 (Table II.1) by the total number per 364 sq m.

Standard deviation in mean leaf galls per plant, and mean stem galls per plant, were regressed on the above stress index at each elevation. Satisfaction of criterion two required that as stress increased, variability in infestation intensity increased. Total leaf galls and total stem galls per two randomly chosen host plants at each elevation were also regressed on the stress index. To restrict the domain to less-than-severely stressed sites as specified by criterion three, plants at 1198 m (with a stress index 4.5× greater than the next larger value) were first dropped. Criterion three depended on infestation intensity increasing as stress increased.

Stepwise multiple regression of 64 plants sampled August 1978 to September 1979 was used to isolate a subset of the independent variables yielding an optimal prediction equation for gall densities. Dependent variables were square root transformed to correct skewed frequency distributions. (Complete data listings are given in Hartman, 1982b.)

Two branches randomly selected from the outer shell and interior of each of 12 plants were also inspected for number of galls per branch. The mean branch-origin height was 27.3 percent (S.D. = 13.092%) of plant height at 1138 m and 52.0 percent (S.D. = 10.70%) of plant height at 1122 m and 1268 m. Because plant sizes differed among elevations, the branches differed in diameter and height above the ground. These disparities were adjusted using analysis of covariance before comparing number of galls per branch (see Hartman, 1982a, Appendix 17).

TABLE II.1 SPATIAL DISTRIBUTION OF *T. STENOLEPIS* AND ITS GALLS
IN THE NEW YORK MOUNTAINS, SEPTEMBER 1977

Transect distance	Elevation	Number <i>T.</i> (per 364 sq m)	Percent young*	Plant size†	Galls per plant		
					Total leaf	New stem	Old stem
0 km	1125 m	29	.138	1	15	9	10
				0	58	58	14
0.4	1140	46	.348	1	20	36	11
				0	15	33	0
0.8	1152	127	.472	0	31	6	2
				0	29	28	11
1.2	1161	50	.280	1	61	37	11
				0	25	9	5
1.6	1177	9	.333	1	64	63	15
				0	12	8	8
2.0	1198	3	0	1	114	57	16
				1	20	39	25

*Vegetation volume less than 42 cu dm per plant.

†0 = young; 1 = mature.

RESULTS

In testing for genetic resistance against gall formation, the null hypothesis was accepted. Samples successively divided with respect to environmental conditions introduced homogeneity in plant-mean gall densities, thereby reducing the variance. Most correlations between variance and sample size were positive and each elevation had several correlation coefficients larger than 0.9. Table II.2 shows *r* values for some representative plant features.

There was thus no justification for positing a genetic polymorphism among plants to account for differences in intensity of leaf or stem gall infestation. In every case, an extraordinarily low or high number of galls was related to extrinsic variables. Results for April 1977 (Table II.3) similarly indicated that in no case did a 95 percent confidence interval include a significant negative correlation coefficient, and only leaf galls at 1268 m lacked a significant positive *r*.

Deductive criteria for the stress-heterogeneity model were tested in turn. Many instances comprised support for criterion one. An environmental factor was usually ineffective in

TABLE II.2 PEARSON CORRELATIONS BETWEEN SAMPLE SIZE AND VARIANCE IN PLANT-MEAN GALL ABUNDANCE:* NEGATIVE TESTS OF THE GENETIC GALL SUSCEPTIBILITY HYPOTHESIS, NEW YORK MOUNTAINS, APRIL 1977 TO APRIL 1978

Elevation	1977 classification	Leaf galls			Old stem galls	Degrees of freedom
		New	Old	Total		
1122 m	octant spacing	.014	-.114	-.278	-.091	5
	neighbor distance	-.065	-.243	-.718	-.285	4
	plant volume	.064	-.261	-.398	.392	5
	<i>Yucca</i> density	.170	.268	-.032	-.299	4
1138	octant spacing	.984	.988	.960	.664	3
	neighbor distance	.980	.862	.944	.350	6
	plant volume	.982	.995	.981	.810	2
	<i>Yucca</i> density	.942	.972	.974	.781	5
1268	octant spacing	.086	-.393	-.521	-.350	4
	neighbor distance	-.135	-.370	-.505	.326	5
	plant volume	-.037	.014	-.278	.194	4
	<i>Yucca</i> density	-.241	-.553	-.574	.068	4

Elevation	1978 classification	Leaf galls			Stem galls			Degrees of freedom
		New	Old	Total	New	Old	Total	
1122 m	neighbor distance	.482	.778	.859	.915	.631	.959	5
	animal activity	.625	.574	.403	.527	.252	.923	6
	sprout density	.384	.824	.371	.363	.512	.793	7
	flower density	.815	.891	.991	.970	.838	.984	2
1138	neighbor distance	.663	.766	.700	.755	.055	.815	5
	animal activity	.799	.512	.970	.518	.307	.687	6
	sprout density	.406	-.011	.937	.797	.824	.577	7
	flower density	.700	.379	.970	.884	.874	.557	6
1268	neighbor distance	.503	.430	.595	.927	.100	.459	6
	animal activity	.464	.030	.404	.865	.055	.132	7
	sprout density	.125	.099	.402	.873	.054	.090	7
	flower density	.575	.519	.801	.979	.211	.665	2

*Square root transformed

explaining gall numbers per plant at the elevation where it reflected the greatest stress. For example, “foliage” predicted gall number well at 1122 m, where 50 percent of all plants were fully-foliated, but poorly at 1138 to 1268 m, where only 18.8-25 percent were as foliated. Likewise, “plant contact” predicted gall number well at 1138 m, the site of an ecotone between a *Yucca/Coleogyne* complex and a *Larrea/Hilaria* community; while it performed poorly at 1122 m where *Larrea* assumed the *Tetradymia* ecological niche and at 1268 m where *Coleogyne* dominated the vegetation (for further examples see Hartman, 1982a, Appendix 9).

Regression of variability in gall density on stress was best-fit by: $S.D. (galls/plant) = 29.502 (\log \text{ stress index}) + 16.459$ ($r(9) = .874, p = 0$).² The data thus supported criterion two. Additional evidence came from sampling conducted April 1977 through June 1979 at two elevations, 1122 m (high stress) and 1138 m (low stress). The standard error in gall numbers, calculated separately for old and new galls, averaged 56.7 percent higher at 1122 m than at 1138 m; every value at 1122 m exceeded its partner at 1138 m, except in June 1979 (where it came to over 80 percent).

Regression of gall density on stress was best-fit by:
[Galls/(2 plants) = 27.412 (log stress index) + 63.405] ($r(8) = .617, p = .0545$).
Criterion three was thus confirmed.

Stepwise regression of environmental features on plant-mean gall abundances showed that the best two, to five, independent variables explained 37.6 percent of the variation in total leaf galls and 60.7 percent each of that in new and old stem galls (Table II.3). The

TABLE II.3 FORWARD STEPWISE MULTIPLE REGRESSION OF GALLS PER PLANT FOR *T. STENOLEPIS* IN THE NEW YORK MOUNTAINS, AUGUST 1978 TO JUNE 1979

Gall type	Predictor variable*	Partial regression coefficient	Simple correlation coefficient
Leaf	Robustness	1.739	.423
	Browse	-1.563	-.297
	Burrow	1.911	.282
	Intercept	6.070	
			Multiple R = .613
Stem			
	New		
	Burrow	1.729	.453
	Flower density	-0.773	-.324
	Foliage dispersal	-0.901	-.312
	Robustness	0.736	.330
	Tightness	0.482	.148
	Intercept	2.207	
			Multiple R = .779
Old	Burrow	3.958	.693
	Robustness	1.142	.483
	Intercept	1.677	
			Multiple R = .737

*The criterion for inclusion in each equation was an F ratio of at least 2.0 in the test for significance of each regression coefficient (number of galls square root transformed)

2. Stem galls at 1198 m were deleted as significant outliers ($t(9) = 9.626, p < .01$) according to the guidelines of Snedecor and Cochran (1967, p. 158). The standard deviation for this point was less than a tenth of that for leaf galls, compared to a population mean of $4.3\times$ greater than for leaf galls. The aberrancy may be due to the occurrence of only mature *Tetradymia* at this elevation.

burrow (more galls) and robustness (more galls) variables were consistently among the five most important for each dependent variable.

Similar analysis of branch-mean gall abundances showed that a subjective "condition" rating was most predictive, which was in turn influenced by tightness, symmetry, amount of growth, amount of flowers, and lack of rodent browse. After controlling for condition, tightness remained an important determinant of branch-mean gall density, but amount of growth became uncorrelated.

To provide objective biological information, a forward stepwise multiple regression equation omitting "condition" was then calculated, with an inclusion criterion of $F = 3.0$: Stem galls/branch = $.947$ (sprout density) - $.876$ (robustness) + $.968$ (tightness) - 1.756 (shrub contact) - $.720$ (symmetry) + $.035$ (subplot density) + 4.386 . As shown, large branch-mean gall densities were best-predicted by copious growth and tightness, whereas lightly-infested plants were robust, contacted by a shrub of another species, and symmetric.

DISCUSSION

Study of *G. tetradymiella* and *Scrobipalpa* gall recruitment opposed the existence in *Tetradymia* of a gall-susceptibility polymorphism. Gall resistance would be demonstrated only if: 1) a host plant bore significantly few old galls; and 2) in an otherwise good year, it bore significantly few new galls relative to other plants in its category. No plant meeting these criteria was found. To explain all-or-nothing galling, the stress-heterogeneity hypothesis was proposed instead, relating variability in gall densities to levels of stress experienced by individual plants. Evidence supported all three criteria of the hypothesis.

A probable explanation for the action of the stress-heterogeneity model is that while soils in humid regions tend to become uniform due to decomposition and transport of

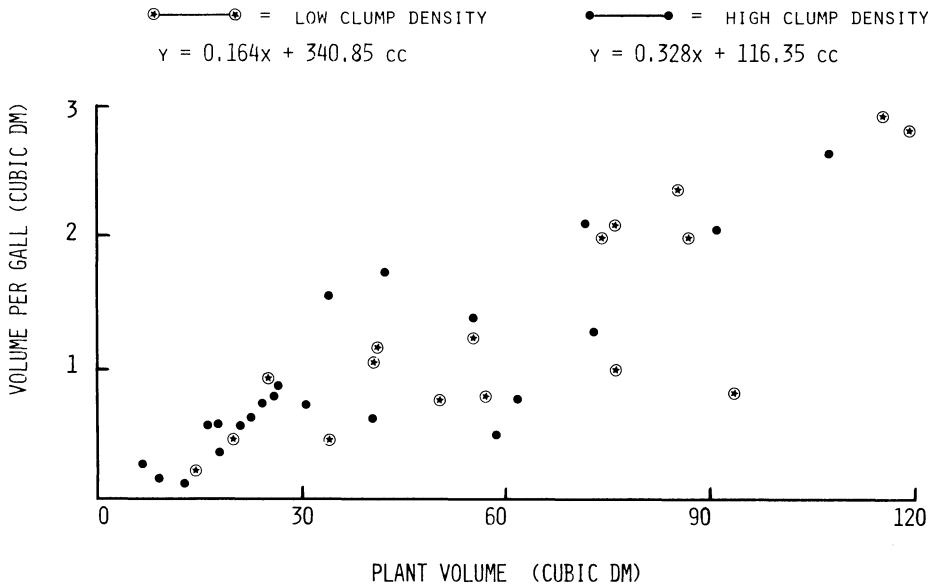


Fig. II.4. Relationship between volume per gall and plant volume, for sparsely and densely clumped *T. stenolepis* in the New York Mountains, April 1977.

soluble matter, desert soils are strongly affected by the nature of the parent-rock or micro-relief (Lemee, 1955). Hence, extreme spatial diversity is preserved, stressful patches exist even in close-to-ideal habitats, and side-by-side neighbors may occupy different patches (cf. Hartman, 1977). Correlations between herbivore infestations and stress may be attributed to the conversion by water-stressed plants of protein reserves into water-soluble forms providing higher-quality food for phytophagous insects (White, 1969).

In accordance with Feeny's (1976) apparency model, sequential combinations of stress-related environmental factors accounted for significant variation in *G. tetradymiella* and *Scrobipalpa* gall densities. The unexpected positive association between animal burrows and galls was explained by investigating ecological determinants of the burrows themselves (Hartman, 1982a, Appendix 19). Predictive factors included *Tetradymia*-specific probability of encounter (low host plant density, distant conspecific neighbors) and vegetation volume (robust host plants, interspecific contact between shrubs). Among plants without burrows, galls were most abundant on robust host plants and least abundant on those which were heavily browsed. Animals apparently removed the same leafy twigs which carried (or might have formed) galls. Among equally-robust and -browsed *Tetradymia*, stem gallmakers favored "tight," concentrated-growth host plants, emphasizing the importance of resource density.

Holding constant basal branch diameter within and among elevations allowed direct comparison of branch-mean gall densities. "Robust" plants had fewer galls per branch, implying that *Gnorimoschema* spread itself evenly throughout the plant (cf. Hartman, 1983c). This interpretation was supported by the positive correlation between volume per gall and plant volume (Fig. II.4). The steeper slope of the trend at high *Tetradymia* densities presumably reflects the greater total available habitat space. Dependence on resource density was again signaled by the positive correlation of gall density with the amount and tightness of new growth. Shrub contact lowered branch-mean gall density, perhaps due to reduced resource density caused by branches intermixing with those of another species (e.g., Robert and Blaisinger, 1978; Tahvanainen and Root, 1972), or competition between shrubs interfering with gall-forming capacity.

The above linear correlation between density of new growth and galls per *branch* implied a geometric increase with resource density in number of galls per *plant*. A plant with copious new growth is more vigorous overall, making individual sprout attractiveness proportional to total sprout number. Solomon (1981) also noted that herbivores may respond to plant density merely as an indicator of plant quality. Plants with more branches would thus also have more galls per branch. This multiplicative effect may contribute to the dramatic variations in gall infestation among neighboring plants conceptualized by the stress-heterogeneity model.

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