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Original papers

Biogeographical gradients in galling species richness

Tests of hypotheses

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Summary. Five hypotheses were invoked to account for variation in galling species number per location on plants of different structural complexity, namely herbs, shrubs, and trees, both in Brazil and USA. The hypotheses were: 1) the altitudinal/latitudinal gradient hypothesis; 2) the harsh environment hypothesis; 3) the plant species richness hypothesis; 4) the host plant area hypothesis; 5) the plant structural complexity hypothesis. The altitudinal and the harsh environment hypotheses were correlated and supported with sample data in both localities, with increasing gall species number as altitude/latitude declined and as sites became hotter and drier. The two hypotheses were separated by studying riparian sites and dry hillside sites at the same elevation in Arizona. Galling species frequency was higher in dry sites than in riparian sites, supporting the harsh environment hypothesis. Of the five hypotheses tested only the harsh environment hypothesis predicted that galling insect species number should vary in response to environmental variables such as moisture and temperature. Temperate shrubs supported more galling species than did other plant types, both in dry and mesic sites. The overall difference between galling species richness for tropical and temperate latitudes was not statistically significant. Free-feeding insect herbivore species exhibited the opposite pattern of species richness to gallers, being more speciose in riparian sites. The present study corroborates the hypothesis that the gall forming habit is an adaptation to harsh or stressful environments, and we describe for the first time broad scale geographical patterns in galling insect species richness.

Key words: Adaptation – Altitudinal gradients – Herbivores – Insect galls – Species richness

The increase of floral and faunal diversity with decreasing latitude and altitude is one of the most well documented biogeographical features of the earth. Hypotheses accounting for these patterns are adequately reviewed by Dobzhansky (1950), Fisher (1960), Pianka (1966), Uetz (1974), Goodman (1975), Thiery (1982), and Price (1984). However, in spite of several long-standing hypotheses which address the maintenance and origin of such trends, mechanisms are poorly understood, and remain largely untested, and many taxa do not fit the general pattern (e.g. aphids, Dixon et al. 1987, and parasite Hymenoptera, Janzen 1981). Therefore, further study and hypothesis testing are needed.

In the southwestern United States casual observations suggested a strong increase in galling insect species diversity with decreasing altitude. Therefore, we undertook this study to see if the pattern really exists and to test for a simple relationship with altitude, or whether the trend was more related to ecological factors other than altitude. Insect galls are good subjects for ecological studies due to their abundance, diversity, and sessile habit, which makes them easier to census than free-feeding herbivores. We studied galling species richness along gradients of latitude, altitude, moisture and temperature, those geographic gradients which historically have yielded the most dramatic contrasts in species diversity. We decided a priori to study pairs of habitats selected for hygrothermal distinctness, and made comparisons of galling species richness on herbs, shrubs, and trees between habitats. The two habitat types were defined as predominantly mesic or xeric, with riparian habitats as mesic, and sites distant from surface water as xeric sites. The distinctions are very strong and clear in the southwest United States. In addition, we studied the variables plant species richness, host plant species area, and plant architecture as the major potential alternative determinants of galling species richness.

These variables were used to address the following hypotheses: 1. The altitudinal/latitudinal hypothesis: as latitude or altitude decline species diversity increases. 2. The harsh environment hypothesis: which predicts that galling species richness will be higher in dry, hygrothermally stressed habitats. 3. The plant species richness hypothesis: which predicts a positive correlation between plant species number and galling species number. 4. The species-area hypothesis: which predicts a positive correlation between host species area and galling species number. 5. The plant architecture (structural complexity) hypothesis: which predicts a positive correlation between plant structural complexity and galling species richness.

Study sites

Temperature sites

Samples were taken on an altitudinal gradient from the top of the San Francisco Peaks at 3843 meters to the lower Sonoran Desert at 305 meters near Phoenix in Arizona, USA. The vertically arranged life zones described by Mer-

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riam (1890, 1899a, b), which occur in the region were studied. The altitudinal gradient had six different plant communities (Lowe 1964), from the bottom to the top: desert, chaparral, pinyon-juniper forest, ponderosa pine forest, spruce-fir forest, and alpine-tundra vegetation. Details concerning each of the vegetation types can be found in Lowe (1964).

Tropical sites

The tropical sites were in Minas Gerais, Brazil. There, samples were taken from Serra do Cipó, near Belo Horizonte, which supports a semi-arid vegetation called cerrado (e.g. Warming 1892, 1908; Eiten 1972, 1978; Coutinho 1978). This vegetation type occurs on poor soils (often with a high aluminum concentration) and woody species are dominated by those that are sclerophyllous (e.g. Goodland 1971a, b; Goodland and Ferri 1979). There is a hygrothermal gradient from the top to the base of the Serra do Cipó (G.W. Fernandes, personal observation; G. Eiten, personal communication), with the base being more stressed hygrothermally than the top.

Methods

In Arizona in 1985, samples were taken from the top of the San Francisco Peaks at 3843 meters (12600 feet), and on each 305 meters (1000 feet) contour down to the low desert at 305 meters (1000 feet) for a total of 13 elevational sites. In each elevational area, north and south slopes were sampled, except at the mountain peak with one sample, making a total of 25 sample sites. In addition, at each elevation, wherever possible, both xeric (away from arroyos and rivers) and riparian sites were sampled. Xeric/mesic comparisons were taken between 915 and 2440 meters for a total of twelve pairwise comparisons. Samples in these sites were repeated in 1986 for galling species and also for free-feeding phytophagous insects. All sites above 2440 m were relatively mesic and sites below 915 m were too disturbed for valid comparisons, so we sampled the full extent of the available range for xeric/mesic comparisons at one altitude.

In the tropical study area, six elevational sites were located at 650, 900, 1050, 1100, 1200, and 1350 meters of altitude. Samples were taken during November and December of 1984, and January 1986. Areas with man-made disturbances such as roads, trails, burns and erosion were avoided.

Ropes and stakes were used to mark transects of 10 meters width. The lengths of the quadrats were variable since samples were based on the numbers of individual plants. Trying to minimize the local plant area effect on gall-forming richness, different numbers of each plant form were sampled: 1000 herbs, 100 shrubs, and 45 trees at each sample site, totaling about 51000 herbs, 5100 shrubs, and 2200 trees in the temperate region, and 9000 herbs, 900 shrubs and 400 trees in the tropical region. One exception to this sample regime was at 650 meters on the tropical site where 500 herbs were surveyed because of the high number of species present. We tested whether our sample size was adequate to detect all galling species on plants of each growth form at all sites. We found that an asymptote between the cumulative number of gall species and the number of plant individuals sampled was reached at all sites for samples smaller than those we used (see Gleason 1922). Ninety percent of all galling species present were recorded by sampling the following number of individual plants: 461.2 ± 288.9 for herbs, 58.5 ± 22.1 for shrubs, and 25.9 ± 12.4 for trees. Sites lacking plants of a particular growth form were not incorporated into analyses for that growth form. The number of galling species for each plant species was recorded. Plant species and gall species were recorded as morphospecies, a standard approach to insect gall species identification (e.g. Felt 1940; Darlington 1975; also see Tavares 1920, 1925). Keys to species in Felt (1940) depend on gall characters.

The host plant species area hypothesis was tested using distributional maps of the host plants in the U.S. (Benson and Darrow 1944; Little 1971, 1976; Anderson 1986). In the statistical analysis we used the continuous area which covered the altitudinal gradient surveyed.

The identified plant species were deposited in the Deaver Herbarium of the Department of Biological Sciences of Northern Arizona University and Departamento de Botânica of the Universidade Federal de Minas Gerais, Brazil.

Free-feeding insect species richness was sampled at sixteen sites at six elevations in Arizona at every 305 m from 915 m to 2440 m above sea level. Ten sweeps of a sweep net through vegetation per sample and five replicates per site were taken, both in xeric and mesic sites. Free feeders were keyed to family and each species received a provisional identification for species, as in the case of plant species.

For direct comparison between tropical and temperate sites altitude was corrected to the equivalent latitude by the standard conversion: 305 m altitude increase is equivalent to 4° increase in latitude (Merriam 1890, 1899a, b; also see Lowe 1964).

Results

Temperate species richness

The altitudinal gradient hypothesis. "Galling Species Richness" (GSR) on herbs, shrubs, woody, and all plants increased with decreasing altitude in dry sites in the 1985 field season. A significant relationship was found between GSR on shrubs and altitude. The decrease in elevation accounted for 73% of the variation in GSR ($r^2=0.73$, $P<0.0005$, $N=21$, Fig. 1). The same pattern was found for GSR on herbs, accounting for 35% of the variation ($r^2=0.35$, $P<0.005$, $N=21$, Fig. 1). Likewise, GSR on woody and all plants showed the same relationships. Hence, decreasing elevation accounted for 66% of variation in GSR on woody plants ($r^2=0.66$, $P<0.0005$, $N=23$, Fig. 2) and 69% on all plants ($r^2=0.69$, $P<0.0005$, $N=25$, Fig. 2). However, GSR on trees alone and altitude were not significantly correlated ($P>0.25$, $N=21$, Fig. 1).

The harsh environment hypothesis. Galling species richness was greater in xeric sites than in mesic sites at the same elevation (Table 1). In addition, in dry sites altitude accounted for significant levels of GSR in all plant groups except trees, but in wet sites no significant relationship were seen (Table 2). Therefore, altitude alone has no explanatory power in mesic sites and no explanatory power for differences in galling species diversity at one elevation between xeric and mesic sites. Hence, we favor the harsh environ-

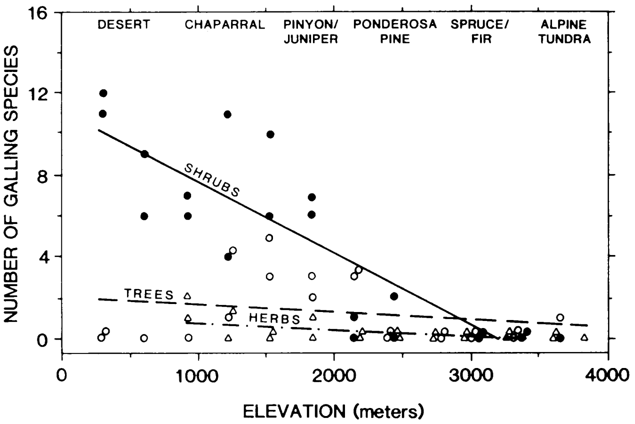

Fig. 1. Regression of galling species richness on shrubs (●——), trees (○– – –), and herbs (△–·–·) as predicted by elevation in dry sites only in Arizona (305 through 3843 meters) in 1985. Vegetation types along the gradient are given at the top of the figure. Riparian sites are not included. Regression equations were: shrubs ($y = 11.1 - 0.00351x$, $r^2 = 0.73$, $P < 0.0005$, $N = 21$), trees ($y = 1.83 - 0.000136x$, $r^2 = 0.04$, $P > 0.25$, $N = 21$), and herbs ($y = 1.04 - 0.000341x$, $r^2 = 0.35$, $P < 0.005$, $N = 21$)

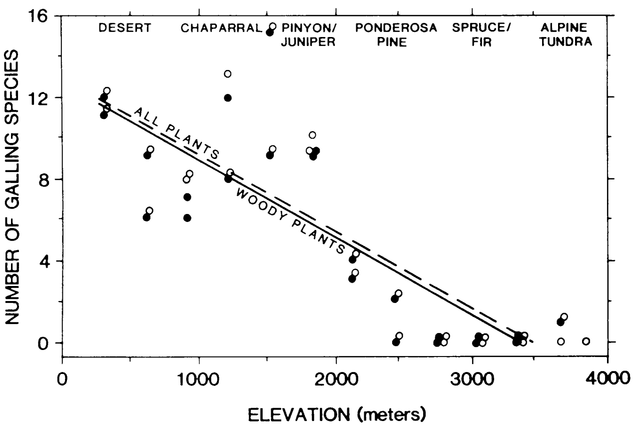

Fig. 2. Regression of galling species richness on all plants (herbs + shrubs + trees (○– – –), and woody plants (●——) as predicted by elevation in dry sites in Arizona (305 through 3843 meters) in 1985. Vegetation types along the gradient are given at the top of the figure. Riparian sites are not included. The regression equations were: all plants ($y = 12.8 - 0.00374x$, $r^2 = 0.69$, $P < 0.0005$, $N = 25$), and woody plants ($y = 12.6 - 0.00378x$, $r^2 = 0.66$, $P < 0.0005$, $N = 23$)

Table 1. Wilcoxon test (Zar 1984) performed for galling species richness on plants of different structural complexity; in xeric and mesic sites along the altitudinal gradient of 915 and 2440 meters in Arizona both in 1985 and 1986. Sample sizes reflect observations removed for ties

Dependent variable (galls on)	Year	N	$\bar{X}$ Galls (Xeric sites)	$\bar{X}$ Galls (Mesic sites)	Wilcoxon test	P_{value}
Herbs	1985	4	0.5	0.5	−9.0	N.S.
	1986	1	0.3	0.0	−7.5	N.S.
Shrubs	1985	11	5.0	2.7	14.5	<0.05
	1986	7	7.3	1.9	3.5	<0.05
Trees	1985	7	2.2	0.8	0.0	<0.01
	1986	2	3.2	1.1	−1.5	<0.01
Woody	1985	10	7.0	3.5	2.5	<0.01
	1986	7	9.6	3.0	3.0	<0.04
All	1985	11	7.4	3.9	6.0	<0.01
	1986	7	9.9	3.0	3.0	<0.04

Table 2. Simple linear regression (Wonnacott and Wonnacott 1986) of galling species richness on altitude in xeric and mesic sites during the field season of 1985 for the elevational sites between 915 and 2440 meters in Arizona. In all cases the degrees of freedom were 1 and 11

Dependent variable (galls on)	Site	r^2	P_{value}	Equation (a ± bx)
Herbs	xeric	0.42	<0.025	1.75 − 0.00080
	mesic	0.30	>0.05	1.75 − 0.00080
Shrubs	xeric	0.48	<0.025	12.9 − 0.00047
	mesic	0.10	>0.25	0.62 + 0.00122
Trees	xeric	0.04	>0.25	3.29 − 0.00063
	mesic	0.09	>0.25	2.25 − 0.00084
Woody	xeric	0.35	<0.05	14.9 − 0.00468
	mesic	0.01	>0.25	2.87 + 0.00037
All	xeric	0.45	<0.025	16.6 − 0.00548
	mesic	0.02	>0.25	4.62 − 0.00042

ment hypothesis and reject the altitudinal gradient hypothesis.

Richness of free-feeding herbivores. Free-feeding insects (i.e., non-gallers and other unconcealed species) were far more speciose in mesic sites than in xeric sites. Free feeders were consistently more numerous in mesic areas than in the xeric areas (Wilcoxon test = 36.0, $P < 0.0005$, $N = 8$, Zar 1984) (Fig. 3). The opposite pattern was observed for gall-making insects in the same time period and on the same elevational gradient (Wilcoxon test = 3.0, $N = 7$, $P < 0.05$, Fig. 3).

These differences between free feeders and gallers support the conclusion above, that gallers are strongly associated with habitats of high hygrothermal stress and have distributions largely distinct from the free feeders, reinforcing the validity of the harsh environment hypothesis.

The plant species richness hypothesis. Galling species richness on shrubs, and woody plants increased with increasing plant species richness in 1985, as predicted by the hypothesis. The increase of GSR on shrubs was highly correlated with increasing shrub species richness ($r^2 = 0.36$, $P < 0.01$, $N = 21$, $y = 0.63 + 1.19x$, Fig. 4). Woody plant species richness accounted for 29% of the variation in GSR on woody plants ($r^2 = 0.29$, $P < 0.01$, $N = 23$, $y = 0.03 + 1.12x$, Fig. 4). On the other hand, herbs, trees, and all plants did not show the same pattern of GSR increasing with increasing plant species richness (PSR); herbs ($r^2 = 0.001$, $P > 0.25$, $N = 21$), trees ($r^2 = 0.08$, $P > 0.10$, $N = 21$), and all plants ($r^2 = 0.04$, $P > 0.25$, $N = 25$).

However, plant species richness was not a convincing explanation of GSR. When galling species richness was observed within host species, or genus, the pattern of GSR

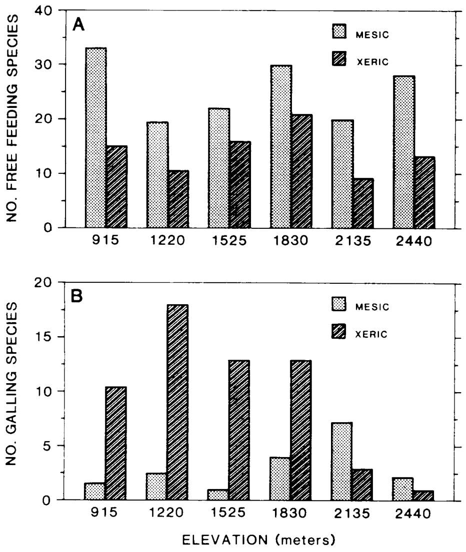

Fig. 3. A Free feeders richness on mesic and xeric sites on the elevational gradient from 915 and 2440 meters in Arizona in 1986. Free feeders richness was significantly greater in mesic sites than xeric sites (Wilcoxon test $=36.0$, $N=8$, $P<0.0005$). All values were based on one sample time, except at 915 and 1220 meters which were based on two samples. **B** Galling species richness on mesic and xeric sites on the elevational gradient from 915 and 2440 meters in Arizona in 1986. Galling species richness was significantly greater in the xeric sites compared to the mesic ones (Wilcoxon test $=3.0$, $P<0.05$, $N=7$). All values are based on one sampling effort, except at 915 meters which is based on two samples

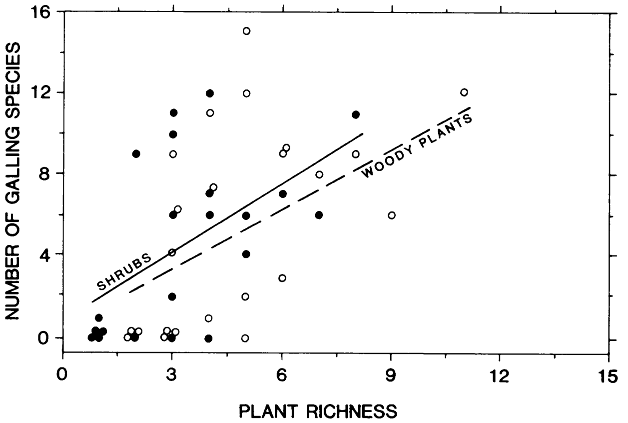

Fig. 4. Regression of galling species number on shrub species number (●——), and on woody species number (○– – –) on the elevational gradient in Arizona (305 through 3843 meters) in 1985. The regression equations are $y=0.63+1.19x$ ($r^2=0.36$, $P<0.01$, $N=21$) for shrubs, and $y=0.03+1.12x$ ($r^2=0.29$, $P<0.01$, $N=23$) for woody plants

was still evident with no change in plant species diversity (Table 3). For example, elevation accounted for 95% of the variation in GSR on *Larrea tridentata* ($F_{1,5}=76.83$, $r^2=0.95$, $P<0.0005$, $y=14.7-0.0131x$). Also, elevation explained 75% of the variation in GSR on *Juniperus* ($F_{1,6}=14.91$, $r^2=0.75$, $P<0.01$, $y=7.29-0.00284x$) and 36% on *Pinus* ($F_{1,11}=5.49$, $r^2=0.36$, $P<0.05$, $y=2.07-0.000651x$). Elevation explained 76% of the variation in GSR on *Quercus* ($F_{1,7}=19.23$, $r^2=0.76$, $P<0.005$, $y=19.7-0.0082x$). For generic comparisons only one species per genus occurred at any one elevation sampled, so plant species diversity did not change. In addition, most galler richness was supported by one species of plant at many sites. For example, at 305 m *Larrea tridentata* supported 92% of all galls, although representing 23% of all plants species; in one site at 1220 m *Quercus turbinella* supported 64% of all galls, although representing only 4% of all plant species.

No significant statistical differences were observed between xeric and mesic sites in the 1986 field season in the species richness of architectural types. Shrubs (Wilcoxon test $=10.5$, $P=1.0$, $N=6$), herbs (Wilcoxon test $=19.5$, $P=0.398$, $N=7$), trees (Wilcoxon test $=10.0$, $P=0.1$, $N=4$), and all plants (Wilcoxon test $=25.0$, $P=0.76$, $N=7$) were equally speciose in xeric and mesic sites. Woody plants were significantly more speciose in mesic sites (Wilcoxon test $=28.0$, $P=0.022$, $N=7$). If plant species richness was an important factor explaining GSR, we would expect a consistently richer flora in xeric sites where gallers were more speciose. However, we found a trend in the opposite direction, since all plant architectural types were slightly more numerous in mesic sites. Once more this shows the weakness of plant species as a factor generating richness of gall-forming insects.

We conclude that plant species number is purely a factor correlated with galling species richness, but with no explanatory power, and therefore reject this hypothesis.

The host plant area hypothesis. This hypothesis was not supported. Log area occupied was calculated for 9 species of representative shrubby plants for which distributional areas were available. This group is the most heavily attacked by gallers in Arizona. The number of gall-forming insects per plant species was regressed against log plant species area and the result showed that only 10% of the variation was accounted for by host plant area and the relationship was negative, not positive as predicted ($r^2=0.10$, $P>0.25$, $N=9$, Table 4).

The plant structural complexity hypothesis. Galling species richness did not increase with increasing plant complexity, i.e., from herbs to shrubs to trees. We found a significant difference in GSR due to plant architecture ($F_{2,95}=20.843$, $P<0.000$) in the USA. In this case, galling species were more numerous on shrubs ($\bar{x}=3.94$, S.E. ± 0.66, Duncan Procedure, $P<0.05$) than on herbs ($\bar{x}=0.31$, S.E. ± 0.11), and on trees ($\bar{x}=1.06$, S.E. ± 0.27). Galling species richness between herbs and trees did not differ statistically ($P>0.05$).

In the tropical sites the number of galling species on each plant group was not significantly different between architectural types ($F_{2,24}=0.475$, $P=0.6276$); herbs ($\bar{x}=4.33$, S.E. ± 0.91), shrubs ($\bar{x}=5.33$, S.E. $=1.26$), and trees ($\bar{x}=3.89$, S.E. $=1.02$). Therefore, we reject this hypothesis.

Tropical species richness

The pattern of increasing GSR with decreasing elevation held for trees, woody plants, and totals for all plant groups in the tropical sites. However, GSR on herbs was mostly explained by variation in herb species richness, and GSR on shrubs was not explained by the studied variables. Stepwise multiple regression analysis of galling species richness on elevation and plant species richness showed that

Table 3. Regression analyses (Wonnacott and Wonnacott 1986) of galling species richness for individual plant species, and genera, along the altitudinal gradient from 305 and 3843 meters in Arizona. Data are from 1985 and 1986

Plant species	Degrees of freedom	F_{value}	r^2	P_{value}	Equation ($a \pm bx$)
Larrea tridentata	1,5	76.83	0.95	<0.0005	$14.7 - 0.01310$
Juniperus	1,6	14.91	0.75	<0.01	$7.29 - 0.00284$
Pinus	1,11	5.49	0.36	<0.05	$2.07 - 0.00065$
Quercus	1,7	19.23	0.76	<0.005	$19.7 - 0.00820$

Table 4. Relationships between galling species richness and log-area of host plant ($r^2 = 0.10$, $P > 0.25$, $N = 9$, $y = 26.4 - 1.79x$)

Host plant species	Area (km^2)	Number of galling species
Atriplex canescens	37820	6
Acacia greggii	156323	4
Chrysothamnus nauseosus spp. *hololeucus*	5025	9
Ephedra viridis	136579	1
Krameria parviflora	160105	4
Larrea tridentata	136783	14
Mimosa biuncifera	57360	1
Quercus turbinella	29059	20
Simondsia chinensis	49166	1

Table 5. Stepwise multiple linear regressions (Wonnacott and Wonnacott 1986) of galling species richness on altitude and plant species richness for tropical plant types on the altitudinal gradient between 650 and 1350 meters (Serra do Cipó, Brazil). Only significant relationships are included. In all cases degrees of freedom were 1 and 7

Dep. variable (galls on)	Predictor variable	F_{value}	r^2	P_{value}
Herbs	Number of herb species	9.0266	0.56	0.0198
Shrubs	–	–	–	–
Trees	Elevation	13.9328	0.67	0.0073
Woody	Elevation	7.6068	0.52	0.0282
All	Elevation	6.8903	0.50	0.0342

elevation was the best predictor ($F_{1,7} = 13.9328$, $r^2 = 0.67$, $P < 0.0073$, Table 5). Again, GSR on woody plants was primarily explained by elevation ($F_{1,7} = 7.6068$, $r^2 = 0.52$, $P < 0.0282$, Table 5). Also, elevation was the best predictor of GSR on all plants ($F_{1,7} = 6.8903$, $r^2 = 0.50$, $P < 0.0342$, Table 5). The increase in herb species richness alone accounted for 56% of the variation in galling species richness on herbaceous plants ($F_{1,7} = 9.0266$, $P < 0.0198$, Table 5). Neither of the entered variables, elevation and shrub species richness, explained the variation of GSR on shrubs.

Tropical vs. temperate galling species richness

There were no statistically significant differences in GSR between tropical and temperate sites ($F_{1,46} = 1.316$, $P = 0.258$), although a trend existed in each plant type for more species in tropical than in temperate regions.

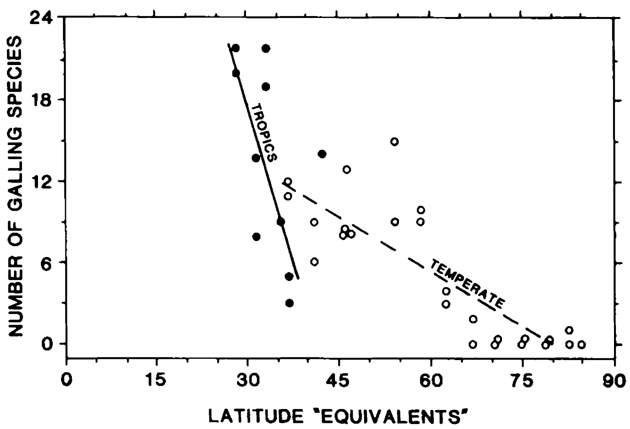

Fig. 5. Tropical (●——) and temperate (o– –) linear regressions of galling species number on latitude corrected for altitude. The equations are: Tropical; $y = 65.0 - 1.57x$ ($r^2 = 0.48$, $P < 0.05$, $N = 9$), and Temperate; $y = 21.6 - 0.269x$ ($r^2 = 0.70$, $P < 0.0005$, $N = 25$)

A simple linear regression of the number of galling species on latitude corrected for altitude clearly showed a trend of increasing galling species frequency with decreasing "latitude" for both tropical and temperate data (Fig. 5). Overall, samples were taken from the equivalents of "latitudes" from 28°30′ through 85°30′. The regression lines show an abrupt increase in galling species number below 35°, although just above 35° tropical samples had fewer galling species than the temperate examples. This probably relates to the more extreme hygrothermal stress in the Sonoran Desert than at high altitudes in the Serra do Cipó.

Discussion

For the first time this study documents strong habitat-related patterns in the distribution of galling insect species, with species increasing as hygrothermal stress increased. In our review of hypotheses on the adaptive nature of insect galls (Price et al. 1986, 1987), the only one predicting such habitat-related differences invoked hygrothermal stress as the most probable factor involved.

Our study documents the pattern, but it does not explain why it should really exist. If gallers can be successful in dry habitats, why should they not be as abundant in wet sites? There must be forces both in ecological and evolutionary time keeping gallers from becoming abundant on plant species in mesic sites. Also, we suspect that galling becomes common in northern latitudes. For example, in

Finnish Lapland (69°N) Vikberg (1970) recorded 16 species of *Pontania* alone, all gallers on willows, so the chances of getting several species in one sample would be high. This, just at the latitude equivalent in our studies where number of species is falling rapidly to one or no species (Fig. 5). Now that we have documented the pattern, we are involved in understanding why, to be reported on later.

It is clear that gallers are responding to plants in ways generally different from free feeders, at the scale we investigated. They are more speciose in dry sites than wet sites (Fig. 3), also they are more common on plants of lower stature than trees, in contrast to other studies on plant architecture (see Lawton 1983). We also suspect that gall faunas will be depauperate in wet tropical forest (personal observations by the authors, Barbara Bentley, Phyllis Coley, and Daniel Janzen), so they will not support general patterns of species richness on latitudinal gradients.

Plant allelochemical diversity and density may also drive richness of galling insect fauna. Taper and Case (1987) showed positive correlations among leaf tannin levels, leaf cynipid gallers richness and abundance. They argued that tannins may aid in the defense of the cynipid larvae either from hyper-parasites, from herbivores, from pathogens or from some combination of these factors (also see Cornell 1983). In addition to Taper and Case's tannin density hypothesis, we could also argue that tannin diversity is a potential factor enhancing insect galling species richness. Tannin diversity, as well as density, may be higher on plants living in stressfull conditions. Muller et al. (1987) reported higher astringent phenol density on plants inhabiting stressfull sites. It will be important to perform correlational studies between plant allelochemical diversity and density, and gall-forming insect richness, and also for free-living insect herbivore richness, as we did with other variables in the experiments reported here.

Galling may well be strongly associated with sclerophylly in the areas we sampled. Gallers are very common in the chaparral of Arizona especially on *Quercus turbinella* with its holly-like leaves, and in the desert on *Larrea tridentata*, on *Atriplex* (Hawkins and Goeden 1984), and similar shrubs. In eastern Australia, dominated by sclerophyllous vegetation, gallers are very common, even at mesic latitudes in coastal areas (personal observation). In the campina vegetation of sclerophyllous shrubs on the depauperate sands along the Rio Negro, Amazonia, the insect fauna is dominated by gallers (Barbara Bentley, personal communication). We will document these patterns in a future publication, but the interesting question will remain on why gallers are less effective in colonizing plants on wet sites in tropical and temperate regions.

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