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Genetic differentiation and phenotypic plasticity in vegetative and reproductive characters of two populations of *Anoda cristata* under incipient domestication

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Abstract. *Anoda cristata* (Malvaceae) is an annual herb of wide distribution in Mexico. It grows as a ruderal, in secondary vegetation. As an agrestal, it grows in different agrohabitats (crop fields of corn, orchards). In the Central region of Mexico the leaves are commonly used for food and are gathered from plants growing in agrohabitats (agrestal), which in turn suggests that this species is becoming domesticated. In this study we show the results of an experiment with two populations (ruderal and agrestal) of *Anoda cristata* collected in Ozumba county, State of Mexico. This experiment attempted to test the hypothesis that: 1) human selection has promoted local differentiation between both populations at the morphological and genetic levels and 2) the management of agrestal populations has promoted a reduction in the amount of genetic variation as a result of human selection. We obtained full sib families of each population by self pollination, and individual plants of each family of each populations, so we obtained full sibs. Individuals of both populations were sown in each of the two contrasting environments, following a reciprocal transplant experiment. Results showed that: 1) there is no genetic differentiation between both populations, 2) there is a plastic response to environmental fluctuation, measured by the response to both environments, and 3) within-population genetic variation exists in both populations in characters related to use by humans. These results suggests little influence of human selection in these characters despite the genetic potential that exists.

Key words: *Anoda cristata*, Food use, Genotype-environment interaction, Human selection, Phenotypic plasticity

Introducción

Anoda cristata is a widely distributed annual weed in Mexico and other countries (from the USA to Bolivia, Argentina and Chile), where it grows naturally. In Mexico, it grows in different environments, ranging from altitudes of 0 to 2650 m.a.s.l., and associated with different types of vegetation such as pine-oak forests, tropical forests and arid lands. In these environments, it grows as a ruderal in disturbed and undisturbed habitats, or an agrestal associated with agrohabitats. As a result of this, it exhibits a wide morphological variation in growth habit and leaf shape (Fryxell 1988; Vangessel & Westra 1997; Vangessel *et al.* 1998).

In spite of its wide distribution, it is only in the central and southern states of Mexico (Michoacán, Guerrero, Oaxaca, Chiapas, San Luis Potosí, Puebla and Mexico), that this species is frequently used by humans, mainly for food but also as medicine (Alcorn 1984; Bye 1981, 1982; Casas *et al.* 1994; Castro 1988; Gómez & Chen de la Cruz 1985; Martínez *et al.* 1995; Vázquez 1986) (Fig. 1).

Previous ethnobotanical studies indicate that people use young, tender leaves and buds, and these can be eaten in combination with beans, squash or corn. Medicinal use is less important. The entire plant is boiled with other plants to prepare a tea to treat stomach inflammation, fever, cough and wounds or as a hair-rinse to reduce balding. Occasionally, the above ground plant is used as fodder (Tab. 1).

In 1995, an ethnobotanical study was developed in the community of Santiago

Fig. 1 - States of México where *Anoda cristata* is reported for food or medicinal use: 1) Chihuahua, 2) San Luis Potosí, 3) State of México, 4) Puebla, 5) Michoacán, 6) Guerrero, 7) Oaxaca, 8) Chiapas.

Tab. 1 - Nutritive value of *Anoda cristata* compared with other vegetables commonly consumed by people.

Species	Ash	Crude fiber	Protein	Nitrogen f.c.
Anoda cristata	2.5	1.1	4.1	8.3
Allium cepa	1.2	1.0	1.87	1.46
Spinacia oleracea	1.6	0.45	2.12	1.72
Vicia faba	0.6	2.27	5.87	13.09
Rumex crispus	1.2	0.90	1.90	3.70
Malva parviflora	2.0	0.88	5.37	3.89
Chenopodium berlandieri	3.7	1.0	4.80	4.0
Portulaca oleracea	2.4	0.77	2.75	2.38

Mamalhuazuca, Ozumba county, in the State of Mexico (Rendón *et al.*, in press) (Fig. 2). We found that people, who name this species "violeta" or "alache", usually consume it during the rainy season, from August to November, either alone or mixed with other species. Plants from agrohabitats are preferred because they are robust and have good leaves. These places have rich organic, moist soils, and because different crops grow there (tomato, corn, squash, bean and medicinal plants), cultural activities (fertilization, irrigation) indirectly benefit individuals of "alache" growing in these sites. People cut the leafy branches near the base of the stem and prefer big, tender and glabrous leaves over small, mature and coarse or pubescent leaves. It means that they select some phenotypes over others. When the plant develops fruits it is considered

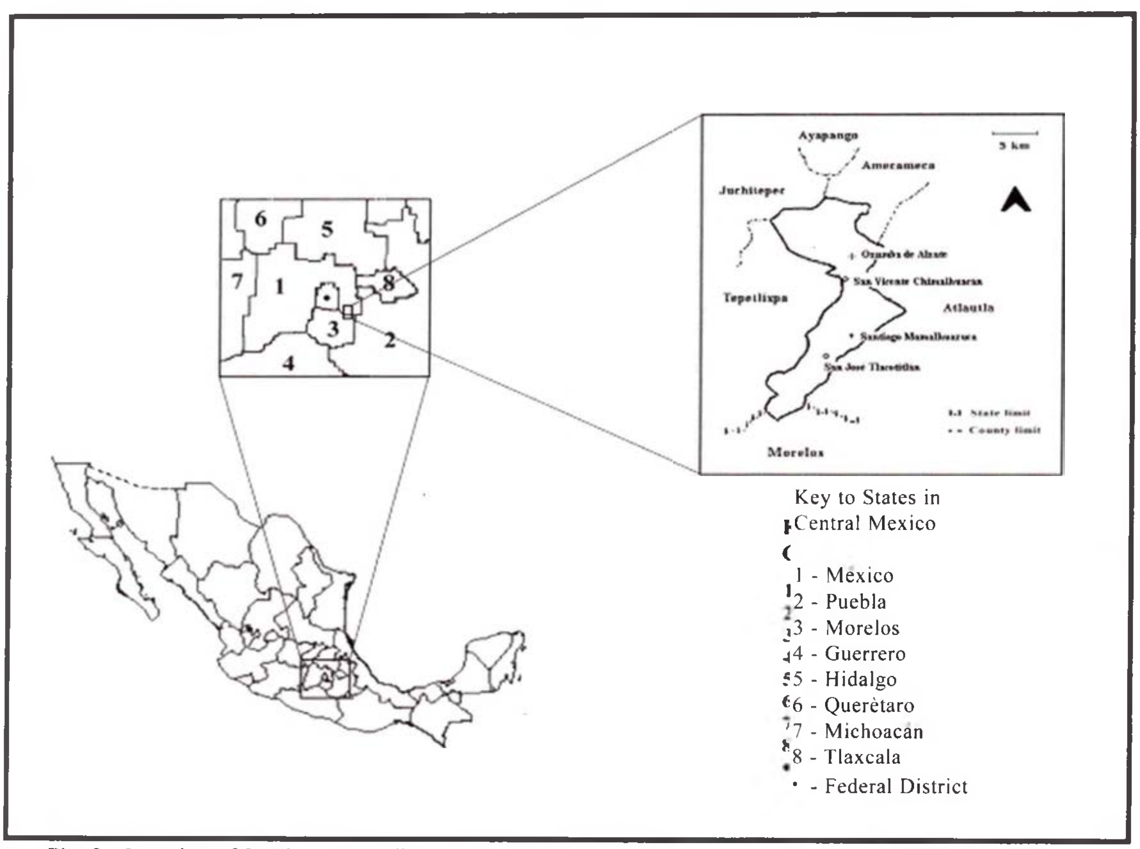

Fig. 2 - Location of Santiago Mamalhuazuca, County of Ozumba, State of México (after Rendón 2000).

unpalatable, because the leaves change color and develop a coarse texture. The most frequent medicinal use was a cough remedy. In this case, flowers and buds are mixed with "gordolobo"(*Gnaphalium*sp.),"bugambilia" (*Bougainvillea* sp.), "tejocote" (*Crataegus pubescens* (HBK) Standl.) and cinnamon (*Cinnamomum* sp.) to prepare an infusion which is sweetened with honey. Fewer people use this species for kidney problems, stomach aches and liver problems associated with hepatitis.

In this area, commercialization of "violeta" occurs during the rainy season and there is a great demand for this plant. People sell the plants in "bunches" (each one consists of 500-700 g fresh weight and costs 20 US cents).Commercialization is a very dynamic event. In some cases, local people from Ozumba and those from nearby communities, gather and sell the plants in the regional market of Ozumba (which has a prehispanic history). In other cases, gatherers go to other markets in neighboring states (Puebla, Morelos and Federal District) (Rendón *et al.*, in press).

Despite the high consumption and commercialization of this species year by year, people do not sow the seeds in the fields or promote it intentionally in the agrohabitats. When the plant produces fruits, people stop eating them, thus plants reach the end of their life cycle without any human manipulation. Seeds disperse from the dry schizocarps and remain in the soil until the next rainy season. Then, they germinate and grow along with other weeds and crops. Even when people practice weeding, "good" and "bad" phenotypes grow alongside, so gatherers cut those phenotypes that satisfy their needs, and leave the rest to grow.

A reciprocal transplant experiment was conducted in 1996 to test the hypothesis that incipient domestication produces 1) population differentiation of characters selected by humans, and/or 2) differentiation might be accompanied of changes in trait plasticity. The first analysis was done using natural progenies, so we compared between populations (Rendón & Núñez-Farfán, in press). We found that: 1) ruderal and agrestal populations of *Anoda cristata* from Santiago Mamalhuazuca differed strongly for vegetative and reproductive traits in the contrasting habitats. In accordance with the statistical analysis, agrestal plants are becoming more specialized to man-made habitats; 2) contrary to expectations, both populations showed the same plastic response, which suggests that this character could be selected prior to the invasion of man-made habitats; 3) it is not possible to affirm that population differentiation occurred solely by human selection and not by other environmental factors; and 4) it is necessary to analyze differences in the response of one phenotype to different environments (known as reaction norms), which in turns give us information about genetic variation within each population (Rendón & Núñez-Farfán, in press) (Fig. 3 and 4).

In this presentation, we report the results of a reciprocal transplant experiment to detect differences in reaction norms (genetic variation) within two contrasting populations of *Anoda cristata* (ruderal vs. agrestal) from Santiago Mamalhuazuca, State of Mexico.

The hypothesis was that if a selective process occurred in the agrestal population, as a result of human selection and habitat specialization, we expect: 1) genetic differentiation and local adaptation; 2) plastic response differences between populations, and between families within each population; and 3) a decrease in genetic variation in agrestal population, thus reaction norms will be homogeneous. The questions we addressed were:

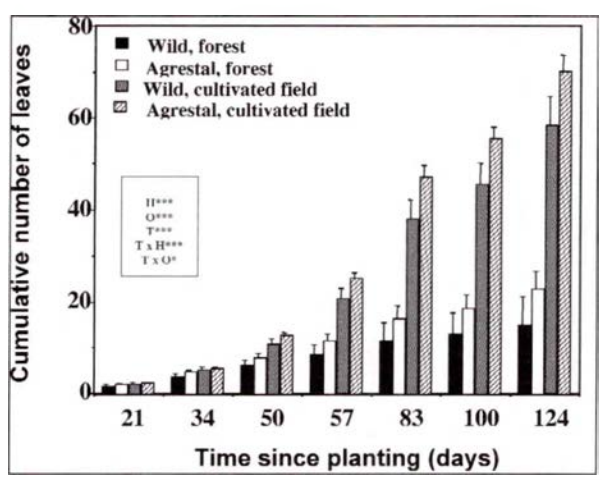

Fig. 3 - Average number of leaves per plant (cumulative) through time in wild (ruderal) and agrestal populations of *Anoda cristata*, growing in two contrasting environments (ANOVA of repeated measures was applied).

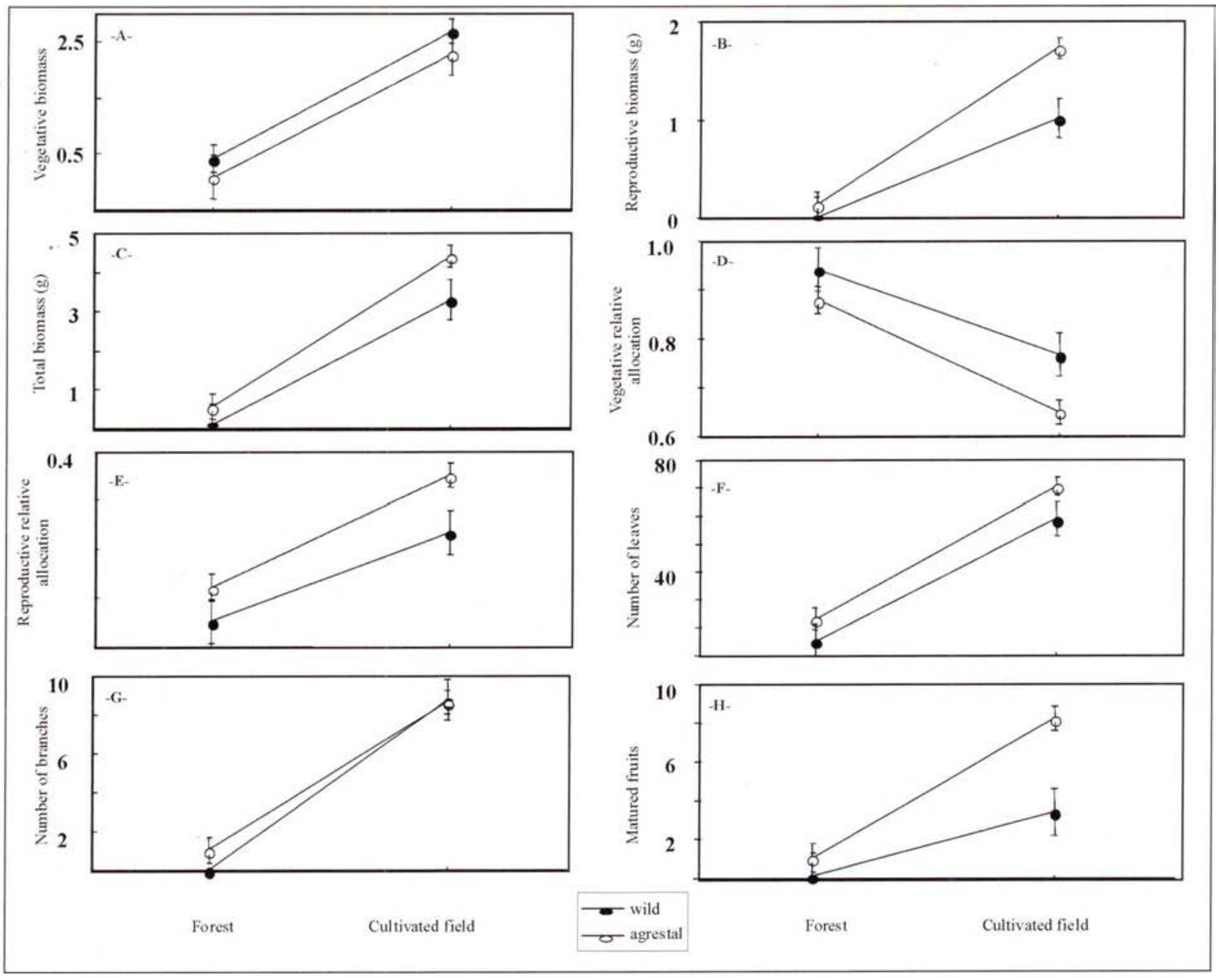

Fig. 4 - Population reaction norms of vegetative, reproductive and allocational characteristics of plants from wild ((ruderal) and agrestal populations of *Anoda cristata* growing in two contrasting environments.

1) are there genetic differences between ruderal and agrestal populations in those vegetative characters related with use, and in those related with fitness; 2) is there genetic variation between populations for those characters?; and 3) are there genetic differences in reaction norms within each population (genotype x environment interaction)?

METHODS

Source of Material

Seeds of both populations of *Anoda cristata* were collected between 1995 and 1996 from individuals growing in two contrasting environments. From each site, seeds of 100 individuals were collected. From these, 30 seeds of different individuals within each population were selected (each one representing a family), weighed and germinated under homogeneous conditions in a controlled - environment chamber (12h light, 28 °C, 12h dark 15 °C; 85% relative humidity). Once the radicle and cotyledons emerged, seedlings were transplanted to pots in a greenhouse (RENDÓN & NÚÑEZ-FARFÁN, in press).

Families

Once the individuals attained the reproductive stage, we made self pollinations to obtain full sibs (they share / of additive variance) (FALCONER & MACKAY 1996). *Anoda cristata* exhibit hermaphrodite flowers (FRYXELL 1988). When immature, stigmas are transparent and folded under the stamens. These mature first (protandry) and release the pollen. Later, the stigmas mature, become erect and turn white, pink or lilac. Protandry facilitated self pollination. We obtained fruits (and in consequence seeds) from 25 families from ruderal population and 26 from agrestal population. From April to June of 1998, seeds were weighed, germinated and shoots obtained. When individuals exhibited 4-6 true leaves, they were transplanted to the experimental environments in Santiago Mamalhuazuca.

Experimental Design

Two contrasting environments, similar to the original ones, were chosen: natural forest (ruderal) and crop field (agrestal). Within each environment, 8-15 individuals of each family were transplanted in a completely randomized design .

Characters Recorded

Ninteen traits corresponding to vegetative characters related with use and those related with fitness were recorded every two weeks (Table 2). From 6-12 leaves of each individual were collected once, dried, measured and weighed to obtain foliar area and foliar mass.

Statistical Analysis

The mean, standard error (SE) and coefficient of variation (CV) were obtained. All data were transformed and analyzed for normality and homocedasticity. Proportions were transformed to the arcsine of their square root. The other data were transformed to their logarithm. Seed weights were used as a covariate to eliminate possible maternal effects on the rest of the characters (SCHMITT 1993). A mixed model analysis of covariance (ANCOVA, SS type III) was applied to each character (SOKAL & ROHLF 1995). Even though seed weight was statistically significant between populations (ruderal, 6.295 mg, e.e. = 0.04; agrestal, 6.570 mg, e.e. = 0.06; SS = 0.00001; F = 14,165 (g.l. = 1, 542); $P < 0.001$; n = 272 in both populations), no significant effect of seed weight over the rest of the characters was detected, so this character was eliminated in the remaining analyses.

Variation of response to environment between and within populations.- Mixed models with three factors were applied (ANOVA, SS type III). Environment and population were fixed factors and family nested in population was the random factor (MILLER & FOWLER 1993).

Statistically significant effects of environment and population indicated phenotypic plasticity and genetic differentiation, respectively. Family nested in population indicate genetic variation within populations. Environment x population interaction indicates that plastic response differs between both populations, and environment x family nested in population interaction indicates differences in response to environment between families (genetic variation for reaction norms) (FRY 1992; SULTAN & BAZZAZ 1993a, b). From the last analysis, patterns of genetic variation within each population were analyzed and reaction norms elaborated (SCHMITT *et al.* 1992; MILLER & FOWLER 1993; SULTAN & BAZZAZ 1993a, b).

RESULTS AND DISCUSSION

Variation between populations in response to environment. The comparison of CV between environments showed that they were higher and the range more extended in the natural forest. Comparison between populations showed that ruderal populations had higher CV, although some characters had higher CV in the agrestal population. Characters with higher CV were those related with branching (secondary and tertiary) and reproduction. Only foliar mass was highly variable in the natural forest (Tab. 2).

Environment was statistically significant for almost all characters, except number of leaves in central axis / axis height and number of leaves in the branch/branch height (foliar area was marginally significant, P = 0.058). Mean values were higher in the crop field. This suggests that individuals of both populations exhibit a plastic response to this factor. This is in accordance with many studies that have demonstrated that annual plants exhibit a plastic response which maximizes their fitness to changing environments (SCHLICHTING 1986; SULTAN & BAZZAZ 1993a).

Even when phenotypic plasticity evolved prior to the invasion of man-made habitats, this character has not been buffered or diminished in agrestal

Tab. 2 - Means value, standar error (in parenthesis) and coefficients of variation (%) of characters measured in ruderal and agrestal populations of *Anoda cristata* growing in two contrasting environments.

Character	Natural Forest				Crop field			
	Ruderal	CV	Agrestal	CV	Ruderal	CV	Agrestal	CV
Number of total leaves	29.317 (1.954)	84.56	27.392 1.953	86.74	103.1 11.08	110.59	98.17 8.34	93.01
Number of total branches	3.09 (0.29)	116.97	3.20 0.31	117.48	13.89 1.63	120.60	16.76 1.63	96.11
Axis height	28.77 (1.55)	68.38	29.74 1.67	68.10	44.55 2.01	52.77	41.36 2.12	49.31
Number of total leaves/axis height	1.47 (0.22)	187.4	1.28 0.12	115.2	2.52 0.23	95.36	2.15 0.14	73.3
Number of branches in axis	4.48 (0.31)	86.56	3.99 0.28	85.75	8.85 0.41	48.04	9.25 0.4	47.43
Number of branches in axis/axis height	0.17 (0.02)	139.88	0.15 0.02	143.84	0.25 0.01	64.23	0.24 0.02	101.64
Number of leaves in axis	9.82 (0.33)	41.97	9.93 0.34	41.25	15.30 0.52	34.81	15.88 0.45	30.81
Number of leaves in axis/axis height	0.493 (0.028)	72.41	0.487 0.029	73.31	0.48 0.027	59.37	0.44 0.025	62.11
Lateral branch height	14.67 (1.298)	112.24	14.46 1.439	121.08	35.37 2.217	64.54	37.93 2.059	59.46
Number of branches (2 and 3) in lateral branch	0.63 (0.09)	200.00	0.44 0.08	220.96	3.68 0.286	79.97	3.45 0.274	87.16
Number of branches (2 and 3) in lateral branch/ lateral branch height	0.024 (0.005)	266.67	0.011 0.002	218.18	0.093 0.007	81.72	0.081 0.005	74.07
Number of leaves in lateral branch	4.09 (0.254)	78.78	3.79 0.241	77.11	9.63 0.414	44.27	9.692 0.36	40.74
Number of leaves in lateral branch/ lateral branch height	0.43 (0.049)	144.76	0.47 0.063	162.45	0.39 0.032	83.42	0.337 0.022	70.03
Number of buds	15.14 (1.187)	99.44	14.08 1.234	106.65	63.132 8.197	133.68	62.64 6.184	108.13
Number of fruits	1.522 (0.248)	206.77	1.405 0.223	192.88	10.425 1.507	148.81	10.642 1.374	141.46
Number of mature fruits	0.404 (0.102)	319.55	0.358 0.081	274.58	4.76 0.857	185.66	4.46 0.668	164.04
Foliar mass	0.028 (0.001)	100.0	0.027 0.001	135.71	0.033 0.001	69.69	0.038 0.001	84.21
Foliar area	470.054 (14.382)	80.02	438.02 12.980	79.69	234.82 10.47	68.68	405.15 12.26	77.34
Specific foliar mass	0.062 (0.00167)	70.54	0.0629 0.00077	52.83	0.0945 0.00159	37.77	0.0958 0.00185	49.63

Tab. 3 - Analysis of variance of vegetative and reproductive characters from families of full-sibs of ruderal and agrestal populations of *Anoda cristata* growing in two contrasting environments (F model type III, fixed effects) (degrees freedom are indicated, F ratio and significance: $p< 0.05$* ; $p< 0.01$** ; $p< 0.001$***).

Character	Environment F (d.f.= 1)	Population F (d.f.= 1)	Family (population) F (d.f.= 49)	E x P F (d.f.= 1)	E x F(P) F (d.f.= 49)	Residual F (d.f.= 434)
Number of total leaves	263.789***	0.008	1.512*	0.589	1.086	0.116
Number of total branches	138.259***	0.447	1.617**	0.089	1.255	0.123
Axis height	55.736***	1.005	1.515*	1.851	0.869	0.109
Number of total leaves/axis height	88.508***	0.978	1.422*	1.195	0.994	0.198
Number of branches in axis	187.982***	0.224	1.308	2.374	1.031	0.011
Number of branches in axis/axis height	74.759***	0.528	0.757	3.737 e-4	1.162	0.035
Number of leaves in axis	162.55***	1.066	1.695**	1.127	0.910	0.035
Number of leaves in axis/axis height	0.662	0.448	1.060	1.254	0.748	0.035
Lateral branch height	176.507***	0.765	1.239	2.092	1.118	0.64
Number of branches (2 and 3) in lateral branch	291.087***	0.003	1.674**	0.489	1.382	0.004
Number of branches (2 and 3) in lateral branch/ lateral branch heigh	t174.292***	0.517	1.065	0.563	0.918	0.028
Number of leaves in lateral branch	297.296***	0.004	1.177	0.996	1.162	0.009
Number of leaves in lateral branch/ lateral branch height	2.456	1.575	0.631	0.382	0.773	0.128
Number of buds	200.932***	0.379	1.476*	1.630	1.145	0.082
Number of fruits	110.515***	0.596	1.994***	1.107	1.481*	0.024
Number of mature fruits	71.664***	0.171	1.994***	0.280	1.745**	0.011
Foliar mass	12.182**	2.878	7.527***	1.572	2.892***	0.003
Foliar area	4.023	1.769	7.488***	2.037	2.700***	39.869
Specific foliar mass	321.100***	0.582	3.087***	0.013	2.345***	1.935 e-6

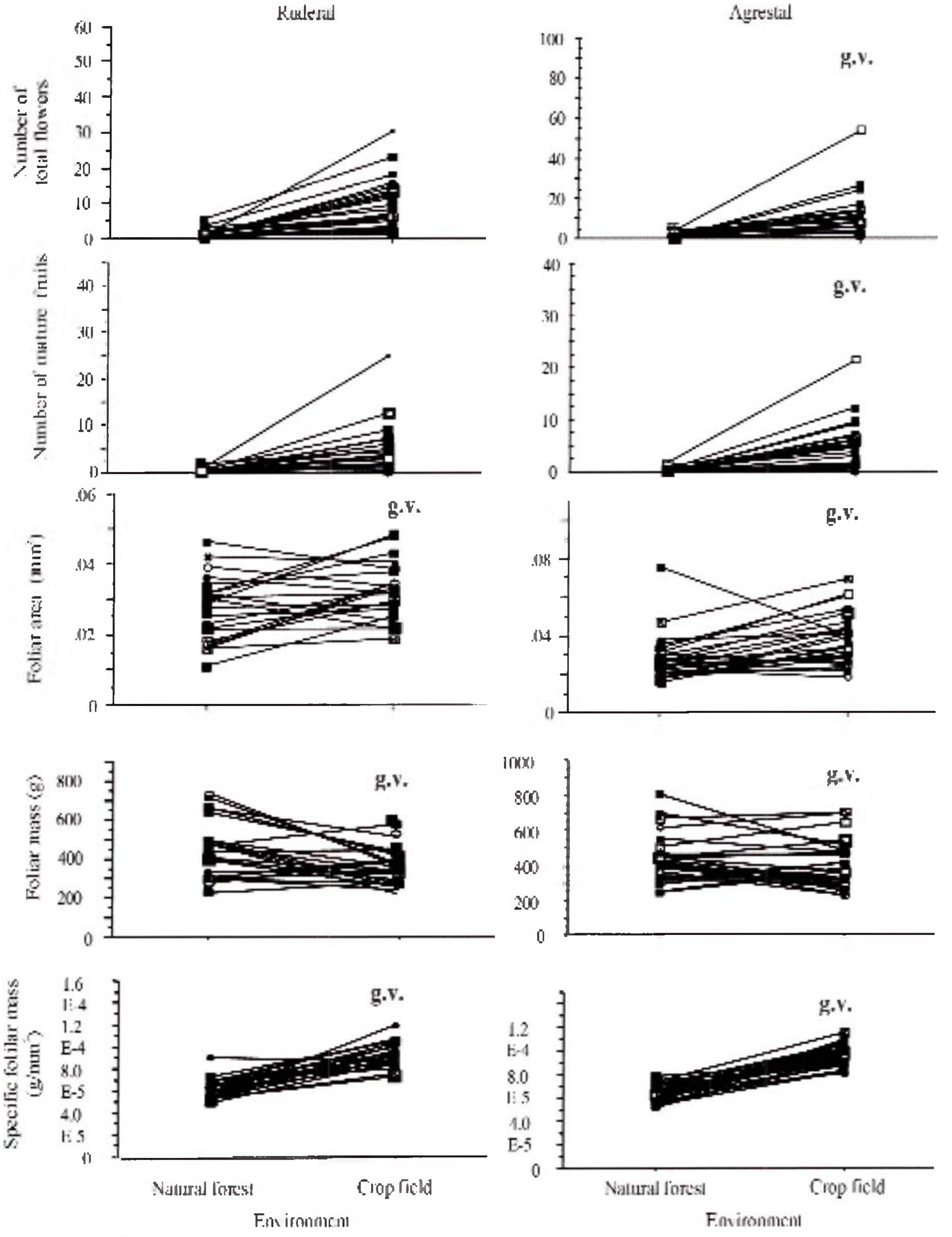

Fig. 5 - Reaction norms of reproductive and foliar characters that showed E x F(P) interaction. These were obtained from full sibs families of ruderal and agrestal populations of *Anoda cristata* growing in a reciprocal transplant experiment.

individuals. Some authors have suggested that phenotypic plasticity is a primary character selected by farmers through unconscious selection, because it facilitates invasion of agrohabitats (Tab. 3) (RENDÓN & NÚÑEZ-FARFÁN, in press).This aspect explains the observed genetic variation within populations, specifically in characters related with fitness, which in theoretical terms should exhibit low genetic variation because selection has eroded this variation. This variation is important because individuals can reproduce under different conditions even in agrohabitats, when cultural activities are applied (e.g., weeding) (Tab. 3).

Genetic variation in foliar characters is important because it is related to photosynthesis and plant growth. Foliar mass, a character related to photosynthetic tissue storage and availability (CHAZDON & KAUFMANN 1993; MIAN *et al.* 1998), exhibited a higher mean value in crop field, while specific foliar mass, a character related with photosynthetic tissue per unit area, was higher in crop field. This could be a response to light intensity, but it indirectly benefits farmers because they obtain more nutrients.

Populations were not statistically significant for any character, which indicates no genetic differentiation between ruderal and agrestal population. There are two possible explanations: 1) both populations have phenotypic plasticity, but agrestal population maximize this response because of physical conditions in agrohabitats, such as reliable water supply or full exposure to the sun; or 2) artificial selection has not happened yet (ANDERSON 1989; BARRETT 1988; HERMANUTZ & WEAVER 1996; SCHLICHTING 1986; SULTAN & BAZZAZ 1993a). Other factors not considered in this study could reduce the possibility of genetic differentiation: 1) reproductive system in *Anoda cristata* exhibits dichogamy, which promotes out crossing and, in consequence, weakens the effect of human selection; 2) agrestal and ruderal populations are not completely isolated one from another, so occasionally gene flow could happen; and 3) frequent environmental fluctuations, which would reduce the possible effect of human selection. Even when agrohabitat is a relative constant environment, seeds collected in two years (1995 and 1996) could be subject to different environmental conditions. Also, we don't know if they are from the same year (Tab. 3).

Reaction norms observed in foliar characters and fitness exhibit genotype x environment interaction (Fig. 5). This aspect is responsible, in part, for the maintenance of genetic variation. Farmers may select, within the agrestal individuals, genotypes with an specific response to one environment, but they never can select the reaction norm (SCHEINER & GOODNIGHT 1984; SULTAN & BAZZAZ 1993a, b; VIA & LANDE 1985), and this means a risk, because is possible that they select genotypes that have a good response to one environment, but a bad response in another. Also, it is possible that artificial selection is too weak to isolate both populations and, finally, it is also possible that they are selecting the best, desirable genotypes, but they do not eliminate the undesirable ones. Thus, any condition that favored contact between ruderal and agrestal populations, or even more, desirable and undesirable agrestal genotypes, always favored maintenance of genetic variation and, in consequence, population differentiation will occur with difficulty.

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