HERITABILITY OF FLORAL TRAITS ESTIMATED WITH REGRESSION FOR *Jaltomata procumbens* (Solanaceae)

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AUTHOR'S CONTRIBUTION
The sole author designed, analyzed and interpreted and prepared the manuscript.

Original Research Article

ABSTRACT

Narrow-sense heritability was estimated for eight morphological traits of one species by regressing F_1 mean trait values on midparent trait values. Parents and F_1 plants of *Jaltomata procumbens*, a neotropical herbaceous perennial with bee-pollinated actinomorphic flowers, were grown in a greenhouse. The seeds sown to grow the parent generation were collected from geographically widespread populations. Estimates of heritability presented in this study are likely biased upward by disassortative mating and, consequently, corrected heritabilities are presented as the slope from regression divided by one plus the Pearson correlation coefficient. All eight floral traits (flowers per inflorescence, sepal and petal length, extent of petal spots, staminal length, extent of staminal filament pubescence, anther length, and stigma diameter) have corrected heritabilities ranging from 0.24 for flowers per inflorescence to 1.0 for the extent of filament pubescence, and thus for *J. procumbens* the traits studied retain the ability to respond to selection if there is genetic exchange among populations.

Keywords: Anther length; flower number; midparent midoffspring regression; narrow-sense heritability; petal spots.

1. INTRODUCTION

Lynch and Walsh [1 p.175] stated that an interesting question yet to be properly addressed is, how does narrow-sense heritability differ among characters (traits)? I considered this question with living plants of *Jaltomata procumbens* (Cav.) J. L. Gentry, an herbaceous perennial of the neotropics. Plants from morphologically distinct, geographic widespread populations were crossed. A priori, I recognized a genetic component to morphological variation: i.e., self-set seeds gave plants that were virtually identical to the parent from which the seeds were collected, and parent plants from different populations were morphologically distinguishable from each other. To quantify evolvability I regressed the mean trait values

of the F_1 on those of the midparents for several morphological traits, estimating narrow-sense heritability from the slopes of the regressions. The traits studied, flower number, sepal and petal length, extent of petal spots, staminal filament length, extent of staminal filament pubescence, anther length, and stigma diameter, are presumably all important in the life history of the species.

2. MATERIALS AND METHODS

Estimates of heritability can be based on midoffspring means regressed on midparent means [2-4]. Estimates of heritability presented in this study are likely biased upwards by both disassortative mating and controlled growing conditions, and so I also present the

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corrected heritability as the slope (from regression) divided by one plus the Pearson correlation coefficient (Visscher, personal communication).

Jaltomata procumbens is a widespread, diploid perennial growing in wild and ruderal habitats as an encouraged weed in corn fields, from Arizona, USA to Ecuador [5]. It is common in Mexico and Central America [6,7; Mione, field work]. The actinomorphic corolla is green; petal spots are darker green and presumably serve as guides to pollinators [see 8], and anthers are yellow (Fig. 1). Nectar droplets accumulate on the base of the corolla, one droplet located at each meeting of the bases of two stamens. Heritability was investigated with source material collected from northern Mexico to eastern Guatemala (Table 1).

Jaltomata procumbens likely has a mixed mating system. Anthers remain closed during the first day the flower is open (protogyny, Fig. 1), allowing manual crossing without the need for emasculation prior to pollination, but flowers were emasculated at the time of pollination to prevent subsequent autogamy. The next day dehisced anthers are positioned 2–4 mm away from the stigma due to the stamens orienting (proximal to distal) away from the style (Fig. 1), with this herkogamy presumably promoting outcrossing. Delayed self-pollination results when stamens become connivent resulting in application of pollen to the stigma [9]. Fruits are abundantly self-set in the absence of pollinators [5], are black to dark purple (rarely green [10]) at maturity, consumed by humans [11], and ripen five to seven weeks after pollination in greenhouse conditions. Honey bees visit the flowers in Mexico [12].

Fig. 1. Protogyny. In the flower on the left filaments are short and anthers have not yet dehisced (day 1). The flower on the right is in the hermaphroditic phase (day 2): Anthers have dehisced and filaments angle (proximal to distal) away from the stigma/style, with this herkogamy presumably promoting outcrossing. Units are mm. Photograph by T. M.; *Mione 401* grown for study in Connecticut, USA from seeds collected in Chiapas, Mexico

Table 1. Geographic origin and collection data of the seed collections used in this study

Collection number	Country, primary political division	Habitat	Altitude m	Voucher specimen
D. Spooner et al. 7035, grown as *320*	Guatemala, Quezaltenango	in sandy soil by edge of corn field	2,680	AGUAT, BIGUA
D. Spooner et al. 7038, grown as *321*	Guatemala, Chiquimula	along a stream	1,930	AGUAT, BIGUA
R. Bye 10083, grown as *506*	Mexico, Chihuahua	roadside	1,675	MEXU
T. Mione 587	Mexico, Distrito Federal	corn field, sunny	2,750	CONN
T. Mione & R. Bye 599	Mexico, Morelos	open sun	2,230	CONN

Table 2. Floral traits measured

No.	Traits	Definition	Units	Developmental stage
1	Flower number	Number of flowers per inflorescence including flowers, flower buds, and pedicel scars	flowers	Inflorescences with at least one open flower
2	Sepal length	Distance of flattened sepal from the base to the tip of the lobe	mm	Open flowers
3	Petal length	Distance of flattened petal from the androecium to the tip of the lobe	mm	Separate measurements for pistillate and hermaphroditic phases
4	Extent of petal spots	(Length of the petal zone having spots divided by petal length) x 100	%	Hermaphroditic stage (after anther dehiscence)
5	Filament length	Distance from base to apex of staminal filament	mm	Hermaphroditic stage (after anther dehiscence)
6	Extent of filament pubescence	(Length of portion of filament having hairs divided by filament length) x 100	%	Hermaphroditic stage (after anther dehiscence)
7	Anther length	Distance from base to apex	ocular units	Open flowers, prior to anther dehiscence
8	Stigma diameter	Longest dimension of the stigmatic surface while the style was horizontal on the microscope's stage plate	mm	Open flowers

Measurements were made on the parent and F_1 generations in consecutive summers (2012–2013) on plants grown (in individual pots) in a University of Connecticut, Storrs, greenhouse, a pollinator-free environment. Sepal, petal, filament, and anther length, and the extent of both petal spots and filament hairs were measured (Table 2). Petal length measurements were made twice, before anthers dehiscence (day one) and after anther dehiscence, because the corolla enlarges after it opens. Stamens were excised, placed on a ruler and filaments and anthers were measured through a microscope. For a given trait, each measurement was made on a different flower (or inflorescence, for 'flower number'). The F_1 data from different crosses of the same two parent collections (crossed in the same direction) were combined. A data point based on midoffspring midparent values was omitted if the parents did not differ significantly for a given trait based on T-tests (not shown). However, the same pair of parents and their midoffspring value were used for the study of other traits when the parents did differ significantly. Hence, the number of plotted points varies among graphs. Sample sizes are shown in the Appendix, presented as the number of plants sampled / the number of measurements.

3. RESULTS

For eight floral traits the slopes of regression lines (Fig. 2, Table 3) are estimates of narrow sense heritability. Most of the traits are measures of size, but extent was measured for petal spots and filament pubescence (see Methods). Flower number had the lowest (0.24) and extent of filament pubescence had the highest (1.0) corrected estimated heritability (Fig. 1, Table 3). At $P = .05$ the slopes of the regression lines are significantly different from zero except for that of flower number; for filament length there were too few data points to calculate a P value (Table 3).

4. DISCUSSION

Narrow-sense heritability (h^2) is the traditional expression for the estimate of the ability of a trait to respond to selection [1 p.175]. It may also be thought of as the "extent to which phenotypes are determined

by genes transmitted from the parents" [13 p.123]. Although not always the best measure of evolvability [14], heritability continues to be reported in part because it allows comparison of traits within and among populations and species [3].

I found the heritability of flower number (0.24) to be lower than that of corolla traits (0.64) as did Ashman and Majetic [15] in a review of 68 studies that included 604 estimates of heritability on 41 species in 21 families (means: Flower number 0.34, corolla traits 0.43). The mean of corrected heritability estimates in

this study (0.6) is markedly higher than Ashman and Majetic's [15] mean heritability for floral traits (0.39). The uniformity of the greenhouse environment likely inflated my estimates of heritability [14,16,17 p. 21). However, Weigensberg and Roff [18] compared laboratory and field estimates of heritability and noted that although laboratory estimates are higher than field estimates they were not significantly different, and so lab estimates should provide a reasonable estimate of heritability in nature. Sixty six percent of the studies reviewed by Ashman and Majetic were also done under controlled conditions.
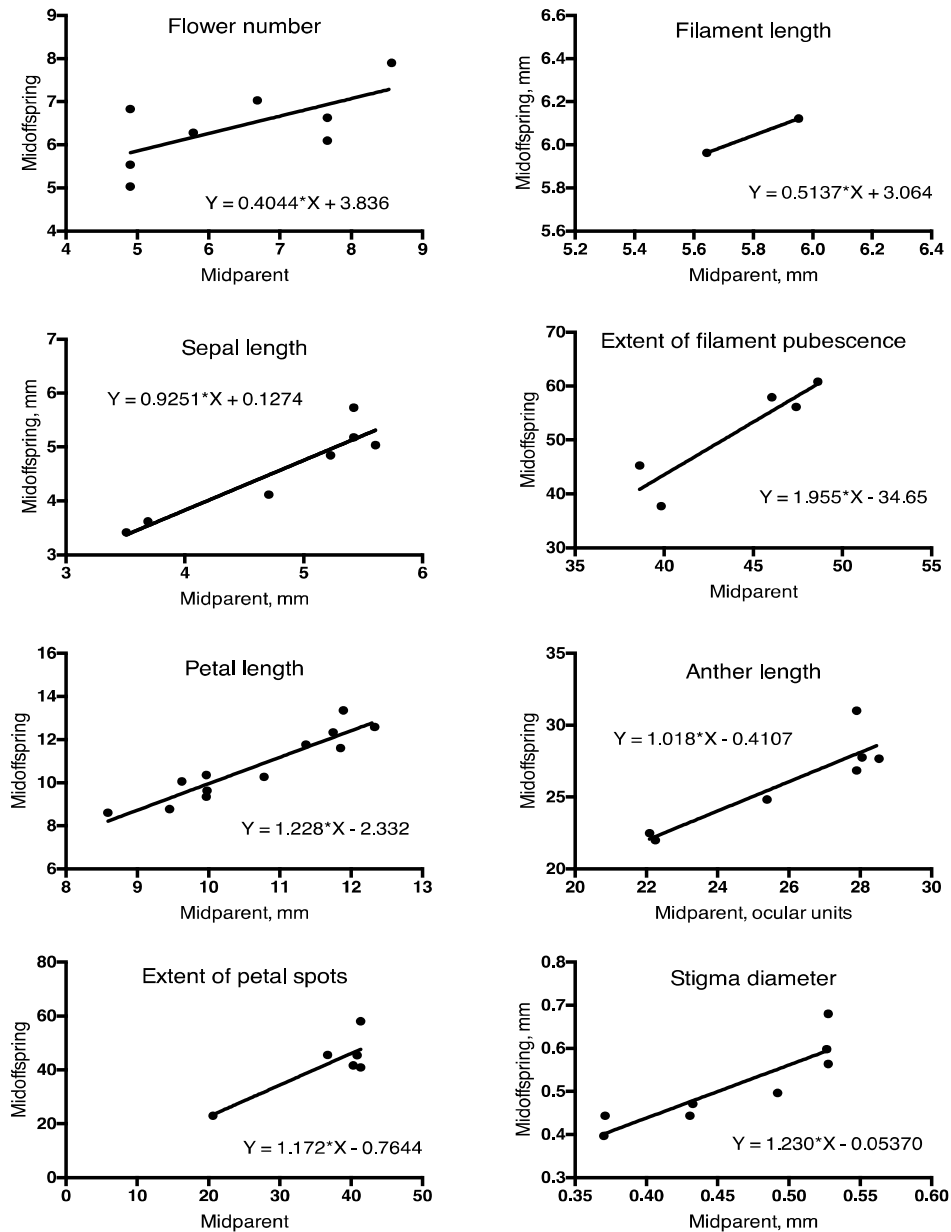

Fig. 2. Scatterplots and linear regressions of floral traits of *Jaltomata procumbens*

Table 3. Narrow-sense heritability and corrected narrow-sense heritability

	Estimate of narrow-sense heritability from the slopes of the regression lines in Fig. 2. Corrected heritability (see Methods).	R square Pearson r Spearman r	Is slope significantly non-zero?
		0.4405	
Flower number	0.40	0.6637	$P = .07$
	0.24	0.5647	
		0.8689	
Sepal length	0.93	0.9322	$P = .002$
	0.48	0.8929	
		0.8741	
Petal length	1.23	0.9349	$P < .0001$
	0.64	0.9107	
		0.7056	
Extent of petal spots	1.17	0.8400	$P = .04$
	0.64	0.3769	
Filament length		1	
	0.51	too few pairs[a]	no data[a]
	no data	too few pairs[a]	
Extent of filament pubescence		0.8408	
	1.96	0.917	$P = .03$
	1.0	0.8000	
Anther length		0.8035	
	1.02	0.8964	$P = .006$
	0.54	0.7748	
		0.7775	
Stigma diameter	1.23	0.8818	$P = .004$
	0.65	0.9518	

a. not applicable because there were only two data points

Heritabilities are considered population parameters [3] but I crossed plants grown from seeds collected in different populations. The deliberate crossing of individuals from morphologically distinct populations (disassortative mating) no doubt also contributed to the magnitude of my heritability estimates. I grew collections I knew to differ for the traits studied because deliberately using one parent with high values and the other parent with low values for a given trait can "improve the precision" of the estimate of heritability [13 p.181]. As concluded for other species [15,19] I found that the floral traits studied retain the capacity to respond to selection if there is genetic exchange among populations.

5. CONCLUSION

I crossed morphologically distinct, geographically widespread populations of one species to regress F_1 trait values on midparent values. For the eight floral traits studied, corrected (see Methods) narrow sense heritability ranged from 0.24 for flower number to 1.0 for the extent of filament pubescence. Thus, the traits studied retain the ability to respond to selection if there is genetic exchange among populations.

COMPETING INTERESTS

Author has declared that no competing interests exist.

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APPENDIX

Appendix Table 1. Anther length

Collection numbers are italicized. In the first column the mean length is above and the number of plants sampled / the number of anthers measured (equals the number of flowers from which anthers were sampled) is below. Lengths are in ocular units; multiply by 0.0825 for mm.

Mean anther length of dam	Mean anther length of sire	Midparent value	F$_1$ Mean anther length
506	*599*		
24.6	31.2	27.9	26.8
2 / 5	2 / 8		4 / 11
587	*321*		
24.9	19.6	22.25	22
2 / 6	2 / 6		8 / 31[a]
506	*321*		
24.6	19.6	22.1	22.5
2 / 5	2 / 6		4 / 16[a]
599	*321*		
31.2	19.6	25.4	24.8
2 / 8	2 / 6		5 / 23
320	*599*		
25.9	31.2	28.6	27.7
2 / 11	2 / 8		12 / 32
599	*587*		
31.2	24.9	28.1	27.8
2 / 8	2 / 6		25 / 56[a]
599	*506*		
31.2	24.6	27.9	31
2 / 8	2 / 5		6 / 6

a. Measurements made on the F$_1$ plants of two or more crosses were pooled

Appendix Table 2. Sepal length

Collection numbers are italicized. In the first column the mean sepal length is above and the number of plants sampled / the number of sepals measured (equals the number of flowers from which sepals were sampled) is below.

Mean sepal length of dam (mm)	Mean sepal length of sire (mm)	Midparent value	F$_1$ Mean sepal length
506	*599*		F$_1$
4.2	6.6	5.4	5.2
2 / 9	2 / 10		4 / 15
599	*506*		F$_1$
6.6	4.2	5.4	5.7
2 / 10	2 / 9		6 / 6
587	*321*		F$_1$
4.6	2.8	3.7	3.6
2 / 8	2 / 13		8 / 30[a]
506	*321*		F$_1$
4.2	2.8	3.5	3.4
2 / 9	2 / 13		4 / 16[a]
320	*599*		F$_1$
3.8	6.6	5.2	4.8
2 / 21	2 / 10		12 / 31
599	*321*		F$_1$
6.6	2.8	4.7	4.1
2 / 10	2 / 13		5 / 18
599	*587*		F$_1$
6.6	4.6	5.6	5.0
2 / 10	2 / 8		28 / 57[a]

a. Measurements made on the F$_1$ plants of two or more crosses were pooled

Appendix Table 3. Petal length

Collection numbers are italicized. In the first column the mean petal length is above and the number of plants sampled / the number of petals measured (equals the number of flowers from which petals were sampled) is below.

Mean petal length in mm, of dam	Mean petal length in mm, of sire	Midparent value	F₁ Mean petal length
506	*599*		
7.8	12.2	10	9.4
2 / 4	2 / 5		4 / 12
506[b]	*599*		
9.2	14.3	11.75	12.3
2 / 4	2 / 7		4 / 12
599	*506*		
12.2	7.8	10	10.35
2 / 5	2 / 4		6 / 6
599[b]	*506*		
14.6	9.2	11.9	13.35
2 / 6	2 / 4		6 / 6
587	*321*		
10.1	9.1	9.6	10.1
2 / 4	2 / 8		7 / 27
320	*506*		
9.4	7.8	8.6	8.6
2 / 7	2 / 4		10 / 23
320[b]	*506*		
13.5	9.2	11.35	11.8
2 / 13	2 / 4		10 / 24
599	*321*		
12.2	6.75	9.5	8.8
2 / 5	2 / 6		5 / 23
599[b]	*321*		
14.6	9.1	11.85	11.6
2 / 6	2 / 8		5 / 18
320	*599*		
9.4	12.2	10.8	10.3
2 / 7	2 / 5		12 / 31
599	*587*		
12.2	7.8	10	9.6
2 / 5	2 / 5		25 / 57[a]
599[b]	*587*		
14.6	10.1	12.35	12.6
2 / 6	2 / 6		28 / 61[a]

a. Measurements made on the F₁ plants of two or more crosses were pooled.
b. Where in sequential rows the same pair of parents is repeated (in the same direction) the first row summarizes measurements made during the pistillate phase (before any of the anthers dehisced) and the second row summarizes measurements made in the hermaphroditic phase (after all anthers dehisced).

Appendix Table 4. Extent of petal spots

Collection numbers are italicized. In the first column the mean extent of petal spots, presumably nectar guides, is above and the number of plants sampled / the number of petals measured (equals the number of flowers from which petals were sampled) is below.

Mean petal spots, of dam	Mean petal spots, of sire	Midparent value	F$_1$ Mean petal spots
506	*599*		
25.3	57.4	41.3	41
2 / 4	2 / 9		4 / 11
320	*506*		
16	25.3	20.6	23
1 / 7	2 / 4		10 / 24[a]
599	*321*		
57.4	24.25	40.8	45.4
2 / 9	2 / 8		5 / 18
320	*599*		
16	57.4	36.7	45.6
1 / 7	2 / 9		12 / 33
599	*587*		
57.4	23.17	40.3	41.7
2 / 9	2 / 6		28 / 61[a]
599	*506*		
57.4	25.3	41.3	58
2 / 9	2 / 4		6 / 6

a. Measurements made on the F$_1$ plants of two or more crosses were pooled

Appendix Table 5. Filament length

Collection numbers are italicized. In the first column the mean filament length is above and the number of plants sampled / the number of filaments measured (equals the number of flowers from which filaments were sampled) is below. Other parental combinations were omitted because the filament lengths of the parents were not significantly different.

Mean filament length of dam, mm	Mean filament length of sire, mm	Midparent value	F$_1$ Mean filament length, mm
320	*506*		
7	4.9	6	6.1
2 / 10	2 / 4		10 / 23
599	*321*		
6.1	5.2	5.6	6
2 / 3	2 / 7		5 / 19

Appendix Table 6. Stigma diameter

Collection numbers are italicized. In the first column the mean stigma diameter is above and the number of plants sampled / the number of stigmata measured (equals the number of flowers from which stigmata were sampled) is below.

Mean stigma diameter of dam, mm	Mean stigma diameter of sire, mm	Midparent value	F$_1$ Mean stigma diameter, mm
506	*599*		
0.47	0.59	0.53	0.56
2 / 8	2 / 9		4 / 13
587	*321*		
0.46	0.28	0.37	0.4
2 / 7	2 / 10		8 / 31[a]
506	*321*		
0.47	0.28	0.37	0.44
2 / 8	2 / 10		4 / 16[a]
320	*506*		
0.4	0.47	0.43	0.44
2 / 13	2 / 8		10 / 24[a]
599	*321*		
0.59	0.28	0.43	0.47
2 / 9	2 / 10		5 / 23
320	*599*		
0.4	0.59	0.49	0.5
2 / 13	2 / 9		12 / 34
599	*587*		
0.59	0.46	0.53	0.6
2 / 9	2 / 7		22 / 39
599	*506*		
0.59	0.47	0.53	0.68
2 / 9	2 / 8		5 / 5

a. Measurements made on the F$_1$ plants of two or more crosses were pooled

Appendix Table 7. Flower number

Collection numbers are italicized. In the first column the mean number of flowers per inflorescence is above and the number of plants sampled / the number of inflorescences counted is below.

Mean number of flowers per inflorescence, of dam	Mean number of flowers per inflorescence, of sire	Midparent value	F_1 Mean flowers per inflorescence in mm
506	*599*		
4	5.8	4.9	5.5
2 / 7	2 / 5		4 / 13
599	*506*		
5.8	4	4.9	6.8
2 / 5	2 / 7		6 / 6
587	*321*		
4	11.3	7.7	6.1
2 / 14	2 / 6		8 / 30[a]
506	*321*		
4	11.3	7.7	6.6
2 / 7	2 / 6		4/ 16[a]
320	*506*		
7.6	4	5.8	6.3
2 / 7	2 / 7		10 / 25[a]
599	*321*		
5.8	11.3	8.6	7.9
2 / 5	2 / 6		5 / 20
320	*599*		
7.6	5.8	6.7	7.0
2 / 7	2 / 5		12 / 30
599	*587*		
5.8	4	4.9	5.0
2 / 5	2 / 14		23 / 42[a]

a. Measurements made on the F_1 plants of two crosses were pooled

Appendix Table 8. Extent of filament pubescence

Collection numbers are italicized. In the first column the mean extent of filament pubescence is above and the number of plants sampled / the number of filaments measured (equals the number of flowers from which filaments were sampled) is below.

Mean petal spots, of dam	Mean petal spots, of sire	Midparent value	F_1 mean petal spots
587	*321*		
19.5	72.6	46	58[a]
1 / 2	2 / 7		8 / 30
506	*321*		
22.25	72.6	47.4	56.1[a]
2 / 4	2 / 7		4 / 16
599	*321*		
24.7	72.6	48.6	60.8
2 / 3	2 / 7		5 / 19
320	*599*		
55	24.7	39.8	37.7
2 / 10	2 / 3		12 / 36
320	*506*		
55	22.25	38.6	45.3[a]
2 / 10	2 / 4		10 / 23

a. Measurements made on the F_1 plants of two crosses were pooled