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Phenotypic response of *Lycopersicon chilense* to water deficit

Respuesta fenotípica de *Lycopersicon chilense* al deficit hídrico

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ABSTRACT

Environmental-induced phenotypic variation in plants is often considered to be a functional response that maximizes fitness in heterogeneous environments. *Lycopersicon chilense,* a tomato species endemic to Atacama Desert, shows altitudinal phenotypics variations in their natural environments, which could be due to different soil water availabilities. It is hypothesized that (a) seeds coming from populations of different environments, cultivated in the same environment, will have similar phenotypes, if populations are not genetically differentiated, and that (b) the different populations subjected to two drought levels should vary their phenotypic constitution with respect to the control groups. The responses of twenty phenotypic traits to different irrigation levels were studied in nine wild populations of *Lycopersicon chilense*. Seeds were collected from populations along an altitudinal gradient (from 20 m to 3,075 m), transferred to a common environment and grown under three soil water conditions: low (80 % FC), moderate (40 % FC) and severe (20 % FC). In spite of the climatic differences in their natural habitat the phenotypic responses of plants growing in the same environment was similar in the nine populations. Significant differences among populations were only observed in three out of twenty traits (fruit fresh weight, fruit volume and number of seeds per fruit). Soil water deficit induced a phenotypic response in twelve characters; among these: root dry weight, cover, number of seeting fruits and number of seeds per fruit showed the highest significance. An interaction between population and drought treatment was found only for fresh weight of fruits, fruit volume and number of seeds per fruit. Our data indicate that the phenotypic response does not differ among populations growing under similar environmental conditions. Probably the phenotypic response of *L. chilense* in their natural habitats is related to physiological and metabolic adjustment rather than genetic variation.

Key words: *Lycopersicon chilense,* phenotypic response, water stress, physiological adjustment, self-organization, wild tomato.

RESUMEN

La variación fenotípica que induce el ambiente en las plantas ha sido considerada como una respuesta que maximiza la adaptación a ambientes heterogéneos. *Lycopersicon chilense,* una especie de tomate endémica del Desierto de Atacama, presenta variaciones fenotípicas altitudinales en sus ambientes naturales, las que podrían deberse a diferentes grados de disponibilidad de agua en el suelo. Se hipotetiza que (a) semillas de poblaciones provenientes de distintos ambientes, crecidas en un ambiente común, presentarán fenotipos semejantes, si las poblaciones no están diferenciadas genéticamente y que (b) las diferentes poblaciones al ser sometidas a dos niveles de sequía deberían variar su constitución fenotípica con respecto al grupo control. Se estudió la respuesta de 20 rasgos fenotípicos en nueve poblaciones de *Lycopersicon chilense* sometidas a distintos niveles de riego. Las semillas fueron colectadas en un gradiente altitudinal (desde los 20 a los 3.075 m de altitud), germinadas, puestas a crecer a las mismas condiciones climáticas y sometidas a tres niveles de riego: bajo (80 % CC), moderado (40 % CC) y severo (20 % CC). A pesar de las diferencias climáticas en sus ambientes naturales, la respuesta fenotípica de las plantas fue semejante en las nueve poblaciones cuando crecieron en un ambiente común. Diferencias significativas entre las poblaciones se encontraron en tres de los 20 rasgos investigados (el número de semillas por fruto, el peso fresco de los frutos y el volumen de los frutos). El déficit hídrico indujo una respuesta fenotípica en 12 caracteres. Los más significantivos fueron: peso seco de las raíces, cobertura, número de frutos cuajados y el número de semillas por fruto. Interacción entre las poblaciones y el tratamiento de déficit hídrico se encontró sólo en el número de semillas por fruto, el peso fresco de los frutos y el volumen de los frutos. Nuestros datos indican que la respuesta fenotípica parece no diferir entre las poblaciones cuando estas crecen bajo condiciones ambientales similares. Probablemente la respuesta fenotípica de *Lycopersicon chilense* en sus ambientes naturales está más relacionada con ajustes fisiológicos y metabólicos que con una diferenciación genética.

Palabras clave: *Lycopersicon chilense,* respuesta fenotípica, déficit hídrico, ajuste fisiológico, auto-organización.

INTRODUCTION

The Atacama Desert is one of the most arid in the world, ranging from southern Ecuador through Peru and northern Chile. Under these extreme environmental conditions, one of the problems for the establishment of the vegetation is the availability of water. Plant development control mechanisms must be sufficiently robust and specific under drought conditions to program organ and tissue development while using a continuous stream of environmental information to fine-tune the outcome (Pahlich 1995). The ability of species to react to changes in their habitats by altering their morphology arises from small deviations in their respective genome potentials, providing the organism with an optimized genetic form that guaranties their optimal performances in accord with their respective environment (Lewontin 1957, Bradshaw 1965, Waddington 1968). Morpho-anatomical mechanisms involve alterations in leaf area, cell wall elasticity, increasing reflective hairs and waxes and decreasing leaf size minimize radiation damage, biomass reduction, increasing shoot-root-ratio, leaf shape, inflorescence development and stature (Montenegro et al. 1980, Squeo et al. 1994, Olivares & Squeo 1999, Torres et al. 2002).

The flexible response of plants to variable environmental conditions by changing physiological and morphological characters can be understood as plasticity (Bradshaw 1965; Jennings & Trewavas 1986). Phenotypic plasticity may be a property character (MacDonald & Chinnappa 1989, Schlichting & Levin 1990, Thompson 1991) and can be heritable (Bradshaw 1965, Scheiner & Lyman 1989). Nevertheless, Sultan & Bazzaz (1993a, 1993b, 1993c) working with genotypes of *Polygonum persicaria*, concluded that in general phenotypic plasticity is not plastic or fixed, but it can vary markedly from one environment to another and therefore, the adjustment to different environments does not necessary require specialized genetic mechanisms. Thus, different genotypes may be phenotypically similar in the same environment.

Lycopersicon chilense Dun (Solanaceae) is a scrub-like perennial wild tomato species, endemic to the Atacama Desert. *L. chilense* is a gametophytic self-incompatible and heterozygous tomato, with flowers and fruits all year-round (Sato 1996, Pezoa 1996). *L. chilense* grows in very different habitats and it is a very successful species, widely distributed over a broad range of altitudes (from the sea level up to high elevation in the Cordillera de Los Andes), and latitudinally extending from Arequipa (16° 40’ S) in Perú to Paposo (25° 00’ S) in northern Chile (Rick & Lamm 1955, Warnock 1991). Populations of *L. chilense* differ phenotypically probably due to the different environments in which they grow (Stewart & Nilsen 1995).

Since water shortage during plant development may be one of the causes of phenotypic variability in wild populations, the variation in twenty phenotypic traits of nine populations of *L. chilense*, collected from the coast to the Cordillera de Los Andes in northern Chile will be evaluated. Considering that phenotypic plasticity is a relevant attribute allowing the plants to respond to wide range of environmental conditions, it is hipothesized that (a) seed of differents provenances show similar phenotypes when grown in common garden, if populations are not genetically differentiated, and that (b) the populations subjected to three levels of soil water irrigation should show some of the differences found in the field.

MATERIAL AND METHODS

Plant material and site characteristics

Seeds were collected from nine wild populations of *L. chilense* in November 1996. The populations were located in contrasting climatic zones along an altitudinal gradient from the coast (20 m) to the Cordillera de Los Andes (3,075 m) in northern Chile (Fig. 1) and stored in a germoplasm-bank under low temperature and low humidity conditions in the Instituto de Investigaciones Agropecuarias (INIA), Centro Regional de Investigación Intihuasi, Vicuña, Chile.

The nine studied populations of *L. chilense* can be ascribed to three physiographic units according their altitudinal localization and climatic condition (Fig. 1). The first unit, composed by populations P1 and P2, grows in the Cordillera de la Costa with a mild uniform coastal climate with scarce rainfall. The evaporation of the sea and the presence of mountains results in a fog zone (camanchaca), which allows the development of plant communities with maximum and minimum temperatures of 28 and 10 °C, respectively, a relative humidity of 70 %, and an average annual precipitation of 5 mm (Rundel et al. 1991, Squeo et al. 1998).

The second unit is the Intermediate Depression, called “Pampas”. It is a flat area of about 60 km wide, located between the Cordillera de La Costa and the Cordillera de Los Andes. This region is dry except for oases and rivers. Another water source for plants are the subterranean reservoirs

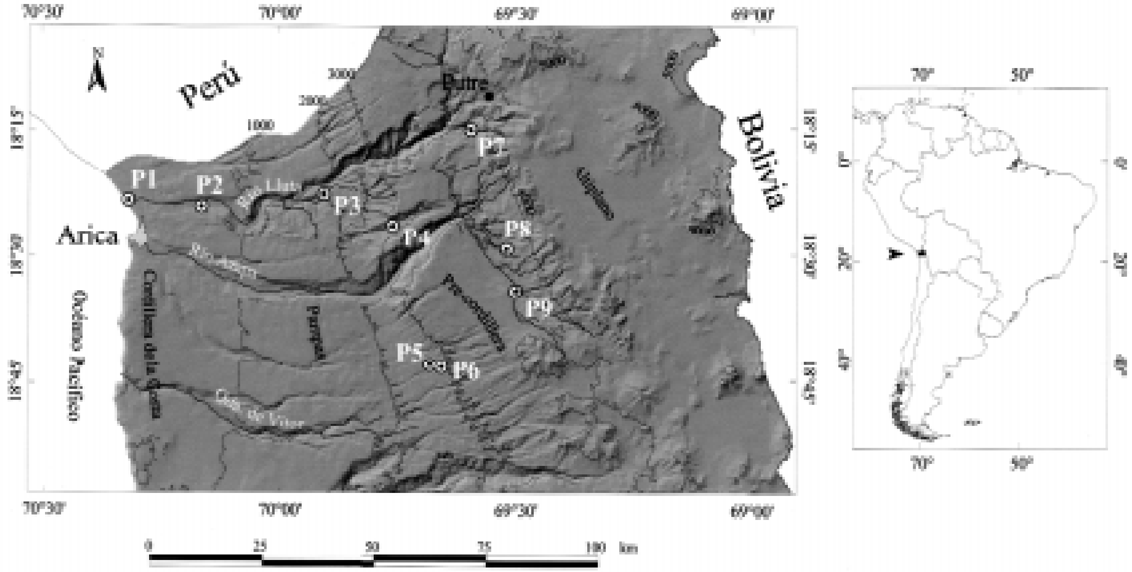

Fig. 1: Seed provenances of nine *Lycopersicon chilense* populations collected in the First Region of Chile (Tarapacá). The Corresponding physiographyc units are indicated.

Procedencia de las semillas de las nueve poblaciones de *Lycopersicon chilense*, recolectadas en la Primera Región de Chile (Tarapacá). Se indican las unidades fisiográficas correspondientes.

built by seeping rainwater. The maximum and minimum temperatures are 32 and 0 °C respectively, the relative humidity is 25 %, and the average annual precipitation is 5 mm (Instituto Geográfico Militar 1985). Populations P3, P4, P5 and P6 grow in this unit.

The populations P7, P8 and P9 grow in the third unit called "Pre-cordillera", which is characterized by low temperatures (maximum and minimum values are 8 and -4 °C, respectively), a relative humidity of 50 % and an annual precipitation of 100 mm. The precipitation is restricted to a short period in summer with monsoonal rainfalls (Aldunate et al. 1983, Arroyo et al. 1988, Pezoa 1996).

Field experiment and experimental design

In January 2000, seeds of nine populations were germinated in Petri dishes, under dark at 15 °C for two weeks, as previously described by Maldonado et al. (2002). Four week old plants were transferred to the experimental field at the Universidad de La Serena, Chile, at an altitude of 80 m (29° 55' S, 71° 15' W). Plants were grown in 25 l pots with a mixture of 2:1 sand:compost, under non-limiting nutrient conditions and irrigated as mentioned below. Distance between plants was 1 m. To reduce the border effect the external rows of plants were not used.

The field experiment was conducted from February to May (summer and fall) 2000 and plants were harvested in May, when 80 % of the first generated fruits were ripen. The climate conditions were: maximum and minimum temperatures of 27 and 5 °C, respectively, mean temperature about 18 °C, and relative humidity about 80 % (Fig. 2). Rains were absent during the experiment period.

Water deficit treatment

To simulate drought, a total of 216 plants of the different populations were subjected to three irrigation treatments. Pots were watered to soil saturation and allowed to drain freely. When 80 % (low water deficit treatment), 40 % (moderate water deficit treatment and 20 % (severe water deficit treatment) water soil potential was reached, the experiment began. Each water regime was maintained by weighing the pots every day and applying the amount of water required to replace water loss by evapotranspiration.

Morphological traits and data analysis

To compare the phenotypic response of the nine populations of *L. chilense* to water deficit, twenty traits were analyzed: (1) leaf dry weight (LDW),

(2) shoot dry weight (SDW), (3) root dry weight (RDW), (4) total biomass (TBI), which is composed of LDW+SDW+RDW, (5) root-shoot-ratio (RSR), (6) shoot length (SLE), (7) plant cover (COV), (8) leaf area index (LAI), (9) number of leaves (NLE), (10) number of floral buds (NFB), (11) number of flowers (NFL), (12) number of seeting fruits (NSE), (13-16) number of fruits with different diameters (13) until 0.5 mm (NF1), (14) 5-10 mm (NF2), (15) 10-15 mm (NF3) and (16) 15-25 mm (NF4), (17) number of total fruits (NTF), (18) fruit fresh weight (FFW), (19) fruit volume (FVO) and (20) number of seeds per fruit (NSF). The number of leaves, flowers and fruits were log-transformed before analyses to ensure data normality and variance uniformity.

Dry weight was obtained from 70 °C oven-dried samples. Cover was estimated assuming an elliptical shape of plants. The leaf area index was determined by quantifying the number of leaf layers in four orientations axes in each plant.

Statistical analysis

Treatments were analysed in a complete block design. Each block consisted of nine populations with three watering treatments (27 plants). Each treatment had eight replicates (eight blocks).

A two-way ANOVA-test was used to compare the response of populations grown under the different irrigation levels. If differences were found,

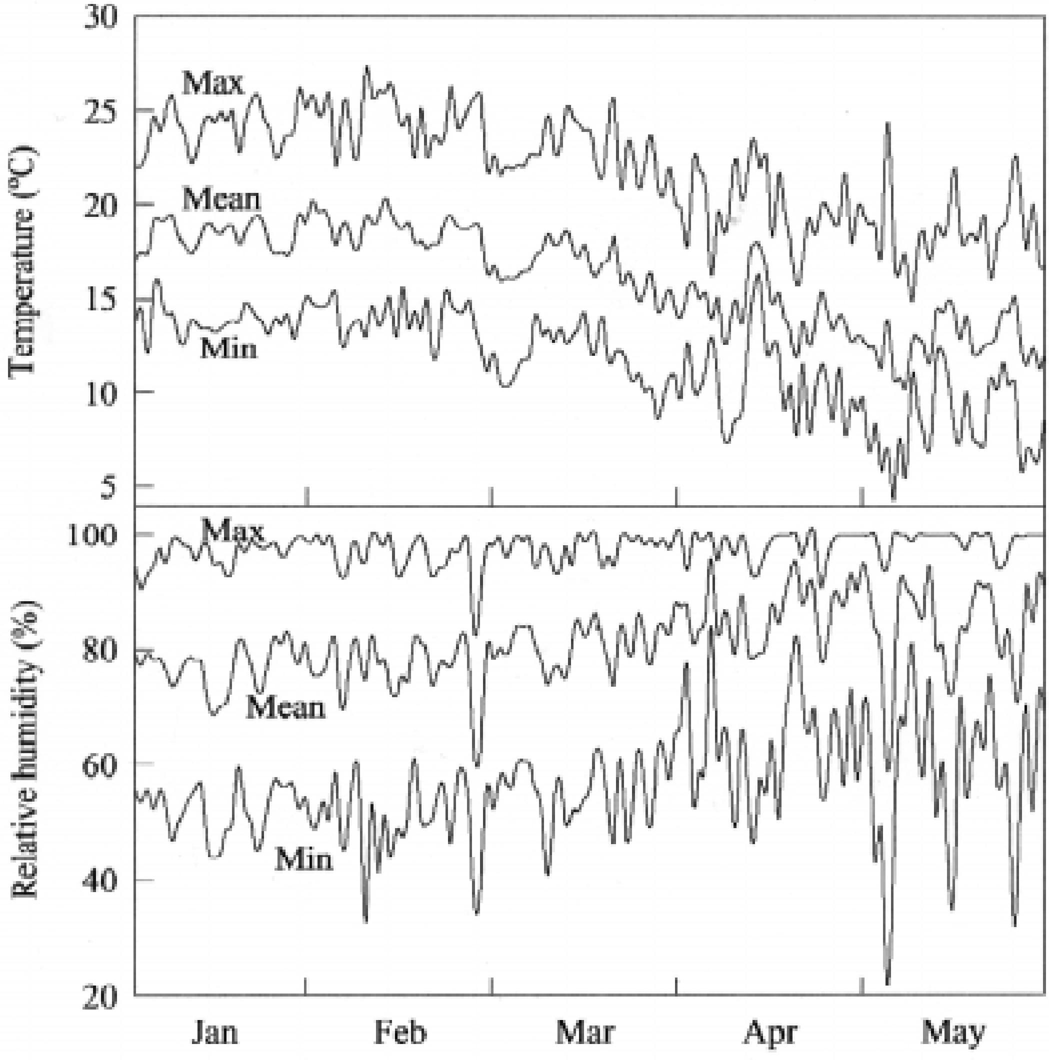

Fig. 2: Maximum and minimum air temperatures and relative humidity from January throughout May (2000). Records are from the climatic station of Universidad de La Serena.

Temperatura del aire y humedad relativa máxima y mínima entre los meses de enero y mayo (2000). Las mediciones fueron realizadas en la estación metereológica de la Universidad de La Serena.

further analysis was performed using the Tukey test for multiple comparison of the traits. The 95 % significance level was used in all cases. All analyses of variance were done using SYSTAT 9 (SPSS Inc., USA 1998).

RESULTS

All populations of *Lycopersicon chilense* were able to grow, flower and develop fruits under the different watering conditions. They did not show any significant differences in seventeen of the twenty studied traits when they were grown under the same environmental condition (Table 1). The vegetative and floral characters were similar among populations. But the traits related with reproduction (FFW, FVO and NSF) differed significantly, being the number of seeds per fruit the most important parameter because it is related to the number of descendants. The populations showing significant differences after an a posteriori test were: (a) P8 < P5 en FFW, (b) P8 < P1 y P5 en FVO, P3 < P4 en NSF (Table 2). However, there was no clear trend in the differences of the reproductive traits and altitudinal provenances of the populations (Fig. 1).

Drought treatment induced a significant phenotypic response in twelve of the twenty traits (Table 1). The vegetative characters which showed differences were: LDW, RDW, TBI, COV, and LAI. The reproductive traits, which showed significant responses, were: NSE, NF2, NF3, NTF, FFV, FVO, and NSF. The watering treatment did not

TABLE 1

Effect of population and treatment on the variation in 20 characters of *Lycopersicon chilense* under drought treatment determined by a two-way ANOVA (P-values as follows: (*) ≤ 0.05; (**) ≤ 0.01, (***) ≤ 0.001; (ns) = not significant. Abbreviations as in Material and Methods (morphological traits and data analysis)

Efecto de la población y el tratamiento sobre la variación de 20 caracteres de *Lycopersicon chilense* bajo deficit hídrico, determinado por ANOVA de dos vías (valores de P de acuerdo a lo siguiente: (*) ≤ 0,05; (**) ≤ 0,01; (***) ≤ 0,001; (ns) = no significativo. Abreviaciones como las descritas en Materiales y Métodos

	Population (df = 8)		Drought treatment (df = 2)		Population x treatment		Error	
	Mean square	F-value	Mean square	F-value	Mean square	F-value	Degees of freedom	Mean square
Vegetative								
LDW	0.309	0.586 ^{ns}	2.618	4.961 **	0.444	0.841 ^{ns}	175	0.528
SDW	6.546	0.875 ^{ns}	6.127	0.819 ^{ns}	4.140	0.554 ^{ns}	175	7.478
RDW	2.584	0.935 ^{ns}	30.268	10.95 ***	2.496	0.903 ^{ns}	175	2.763
TBI	14.812	0.878 ^{ns}	90.086	5.338 **	10.674	0.632 ^{ns}	174	16.877
SLE	63.832	1.156 ^{ns}	65.274	1.182 ^{ns}	38.873	0.704 ^{ns}	173	55.225
RSR	0.480	1.123 ^{ns}	0.229	0.589 ^{ns}	0.166	0.427 ^{ns}	174	0.386
COV	0.899	1.716 ^{ns}	6.454	12.32 ***	0.506	0.966 ^{ns}	174	0.524
LAI	0.070	0.432 ^{ns}	0.568	3.481 *	0.125	0.767 ^{ns}	173	0.163
NLE	0.453	1.524 ^{ns}	0.660	2.221 ^{ns}	0.345	1.160 ^{ns}	176	0.297
Floral								
NBF	1.783	1.059 ^{ns}	2.042	1.213 ^{ns}	1.286	0.764 ^{ns}	176	1.683
NFL	0.246	0.477 ^{ns}	0.769	1.493 ^{ns}	0.666	1.292 ^{ns}	176	0.515
Fruits and Seeds								
NSE	2.462	1.752 ^{ns}	11.462	8.158 ***	0.667	0.475 ^{ns}	176	1.405
NF1	1.697	1.637 ^{ns}	2.168	2.092 ^{ns}	1.028	0.992 ^{ns}	176	1.036
NF2	1.226	0.978 ^{ns}	5.753	4.592 *	0.634	0.506 ^{ns}	176	1.253
NF3	0.599	0.499 ^{ns}	3.751	3.126 *	0.621	0.517 ^{ns}	176	1.200
NF4	0.051	0.610 ^{ns}	0.131	1.579 ^{ns}	0.118	1.429 ^{ns}	176	0.083
NTF	1.117	1.150 ^{ns}	5.961	6.136 **	0.510	0.525 ^{ns}	176	0.972
FFW	0.776	2.058 *	1.308	3.469 *	1.182	3.135 ***	1076	0.377
FVO	2.551	3.156 *	4.204	5.199 **	1.452	1.796 *	1076	0.808
NSF	2.331	1.995 *	14.115	12.076 ***	3.593	3.074 ***	1076	1.169

Weight (g), SLE (cm), COV (m^2), FVO (cm^3)

TABLA 2

Mean (± SE) values of the three traits among the nine populations. Different letters next to the values indicate differences between the populations by the Tukey test at the significance level of P ≤ 0.05. Abbreviations as in Material and Methods (morphological traits and data analysis)

Media (± EE) de tres caracteres entre las nueve poblaciones. Letras diferentes al lado de los valores indican diferencias entre las poblaciones luego de utilizar la prueba de Tukey con un nivel de significancia de P ≤ 0,05. Abreviaciones como las descritas en Materiales y Métodos

Population	FFW (g)	FVO (mm^3)	NSF
P1	0.98 ± 0.10^{ab}	0.18 ± 0.005 a	39 ± 1.1^{ab}
P2	0.91 ± 0.04^{ab}	0.12 ± 0.004^{ab}	35 ± 1.2^{ab}
P3	0.88 ± 0.06^{ab}	0.12 ± 0.005^{ab}	28 ± 1.5^{a}
P4	0.86 ± 0.04^{ab}	0.11 ± 0.004^{ab}	45 ± 1.0^{b}
P5	1.00 ± 0.06^{a}	0.13 ± 0.005^{a}	39 ± 1.1^{ab}
P6	0.95 ± 0.04^{ab}	0.13 ± 0.004^{ab}	36 ± 1.0^{ab}
P7	0.88 ± 0.04^{ab}	0.12 ± 0.004^{ab}	39 ± 1.2^{ab}
P8	0.74 ± 0.04^{b}	0.10 ± 0.003^{b}	35 ± 1.2^{ab}
P9	0.87 ± 0.04^{ab}	0.12 ± 0.004^{ab}	40 ± 1.1^{ab}

induce any effect in floral parameters in contrast to the vegetative and fruit-associated traits. The severe soil water deficit treatment caused a significant decreased of 12 parameters, but LAI, compared to the 80 % FC (Table 3).

The traits with the highest watering-induced response were: RDW, COV, NSE and NSF (P 0.001).

The response of the different populations to the watering treatment can be divided in two groups. The first group (RDW, TBI and COV) showed a similar response under severe and moderate water treatment but differed at 80 % FC. A second group (LAI, NF3, NTF, NSF, LDW, NSE, NF2, FFW and FVO) did not show differences under moderate and low drought treatment but differed from severe conditions.

An interaction between population and irrigation was only found for reproductive traits (FFW, FVO and NSF). The fruit-associated properties (FVO, FFW and NFS) showed significant differences in all investigated variables (population, drought treatment and population x treatment).

DISCUSSION

The capacity of *Lycopersicon chilense* to grow in its natural habitat under different environmental conditions is associated to a wide phenotypic plasticity (Rick & Lamm 1955). A species can persist in a heterogeneous environment either due to a flexible phenotype or genetic variations among individuals of a population (Scheiner & Goodnight 1984).

The plastic response of plants to their heterogeneous habitat and temporal changes in the environment may have an influence on the genetic variation, the selection and the evolutionary drift (Sultan 1987, Sultan & Bazzaz 1993a, 1993b, 1993c, Redbo-Torstensson 1994, Pigliucci & Schlichting 1996). The results of our studies, however, appear to indicate that the phenotypic plasticity observed in wild plants of *L. chilense* is not a result of genetic variation.

In a common garden experiment, the plastic response among nine populations originating from different elevations was similar. No variation was found in seventeen of twenty traits. All populations were able to develop a common pattern of vegetative, floral and fruit-associated characters (Table 1). Our results demonstrate that the altitudinal phenotypic differences found in the field, as those reported by Steward & Nilsen (1995) disappear when the different populations are growing under the same environmental conditions.

How did the nine investigated populations show a relatively constant phenotypic response, even though they grow in their natural environment with a enormous variability of moisture, nutrient, light, and soil? This may result either from genetic uniformity of the wild populations, which means that the evolutionary selection is not advanced, or that the physiological cost or pressure is not high enough to share the populations (Sultan 1992). The existence of such phenotypical breadth within populations requires that individual plasticity may be recognized in physiological and morphological changes as a mayor aspect of plant diversity (Bradshaw 1965, Jennings & Trewava 1986, Sultan and Bazazz 1993c).

The water deficit treatment induced a phenotypic response in *L. chilense*. Twelve of twenty traits were changed significantly by treatments. Nearly all vegetative and reproductive characters decreased with decreasing field capacity. The severe water deficit treatment (20 % FC) had a negative effect on growth, fruit number and seed per fruit of *L. chilense*, but did not suppress the reproductive development of flowers and fruits.

If NSF rather decreases by severe water deficit treatment, we have found a maternal effect of the drought on the seed development. Seeds coming from plants subjected to water deficit germinate faster and under more negative water potential that well irrigated seeds. This could be an advantage when the climatic conditions are favorable for germination (Maldonado et al. 2002).

Our results show that plants adjust their reproductive load when faced to severe water deficit treatment by abortions of the immature fruits rather than the previous phenophases. Likewise, flower and leaf number did not change against the water deficit imposed. The adjustment in this case is due to a reduction of leaf size which translates in a lower leaf biomass (Table 3).

Unexpectedly, RDW increased with high irrigation. In contrast to our result, many studies reported that in plants grown under water deficit, the root-shoot-ratio increases, as a result of increasing the root system (Sharp & Davis 1985). *L. chilense* produced more leaves and root biomass, fruits and seeds per fruit with more water. A similar response has been observed in geophytes from the Atacama Desert (Gutiérrez 1993).

TABLE 3

Mean (± SE) values for the twenty traits of *L. chilense* under water deficit treatment. The severe, moderate and low values corresponding to 20, 40 and 80 % FC. Different letters next to the values indicate differences between the treatment by the Tukey test at the significance level of $P < 0.05$; (ns) = not significant. Abbreviations as in Material and Methods (morphological traits and data analysis)

Media (± EE) de 20 rasgos de *L. chilense* bajo condiciones de déficit hídrico. Severo, moderado y bajo que corresponde a 20, 40 y 80 % CC. Letras diferentes al lado de los valores indican diferencias entre las poblaciones luego de utilizar la prueba de Tukey con un nivel de significancia de $P < 0,05$; (ns) = no significativo. Abreviaciones como las descritas en materiales y métodos

	Water deficit treatment		
Trait	Severe	Moderate	Low
Vegetative			
LDW	1.23 ± 0.09^{a}	1.39 ± 0.07^{b}	1.61 ± 0.10^{b}
SDW^{ns}	3.11 ± 0.49	3.09 ± 0.20	3.57 ± 0.19
RDW	3.90 ± 0.2^{a}	4.37 ± 0.18^{a}	5.17 ± 0.22^{b}
TBI	8.24 ± 0.65^{a}	8.85 ± 0.40^{a}	10.36 ± 0.44^{b}
SLE^{ns}	22.85 ± 0.90	21.52 ± 0.89	21.14 ± 0.91
RSR^{ns}	1.67 ± 0.07	1.65 ± 0.08	1.60 ± 0.07
COV	0.10 ± 0.00^{a}	0.13 ± 0.001^{a}	0.28 ± 0.00^{b}
LAI	1.92 ± 0.05^{a}	1.75 ± 0.04^{b}	1.74 ± 0.05^{b}
NLE^{ns}	57.16 ± 3.74	48.19 ± 2.07	49.27 ± 2.19
Floral			
NBF^{ns}	7.44 ± 1.88	4.52 ± 0.91	5.05 ± 1.52
NFL^{ns}	0.66 ± 0.25	1.49 ± 0.44	1.21 ± 0.36
Fruits and seeds			
NSE	5.50 ± 0.88^{a}	10.17 ± 1.50^{b}	13.43 ± 1.67^{b}
NF1^{ns}	6.99 ± 0.84	9.00 ± 1.20	10.48 ± 1.16
NF2	13.65 ± 1.45^{a}	17.78 ± 1.51^{b}	24.34 ± 2.27^{b}
NF3	1.75 ± 0.39^{a}	4.55 ± 0.86^{b}	4.52 ± 0.96^{b}
NF4^{ns}	0.06 ± 0.00	0.26 ± 0.23	0.09 ± 0.00
NTF	22.44 ± 1.86^{a}	31.59 ± 2.30^{b}	39.43 ± 3.00^{b}
FFW	0.82 ± 0.03^{a}	0.92 ± 0.03^{b}	0.92 ± 0.04^{b}
FVO	642.33 ± 25.1^{a}	707.95 ± 20.5^{b}	666.87 ± 19.6^{b}
NSF	46.22 ± 1.55^{a}	51.97 ± 1.18^{b}	52.39 ± 1.24^{b}

Weight (g), COV (m^2), SLE (cm), FVO (mm^3)

This implies that *L. chilense* developed a successful strategy to survive in an extremely harsh environment and can be considered a drought tolerant plant. Unfortunately ecophysiological parameters of *L. chilense* in their natural habitats have not been described in order to associate the obtained results with field conditions.

The populations of *L. chilense* responded to this severe environmental condition with the best fitness parameters through metabolic adjustment. Pahlich (1995) suggested that the ability of plants to tolerate water deficit is a self-organization process, where all cell functions which are in a thermodynamic balances sense are disturbed and in the metabolic reaction net a search for new stable states is initiated. The initial destabilization of functions is followed by normalization if new stables states can be established. The ontogenetic development of plants and the stress induced metabolic transition must be viewed as a sequence of passages over thresholds (Maldonado et al. 1997).

This may explain why the plastic response of *L. chilense* traits did not show a linear dependence on soil irrigation level. The response was similar under low and moderate drought treatment in most of the studied traits. In this case *L. chilense* has maintained the same stable state from low to moderate water deficit, but a severe treatment exceeded the range of metabolic functioning (steady state) and a new phenotypic response is established.

This response may be explained by theoretical concepts such as “the metabolic control” (Kacser & Burn 1973, Rees & Hill 1994) and the autopoietic theory (Maturana & Varela 1972). Both theories assume that phenotypic changes are possible if in front of a perturbation the system which is auto regulated shifts towards a new steady state or autopoietic space. However, there is not evidence of changes, such as between low and moderate water deficit plant. This would suggest that changes occur when certain internal thresholds are overcome, generating changes in the structures but not in the system organization, seen as an unit (Atkinson 1986, Reich & Selkov 1981, Pahlich 1995, Maldonado & Pahlich 1997).

The differences in response towards environmental conditions from the populations of *Lycopersicon chilense* may be the result of a metabolic flexibility, which most likely results from quantitative rather than qualitative genome differences. Thus facultative metabolic adjustment can be expected instead of genetic specialization.

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