

Morphology, phenology and agronomic traits of two wild Mexican common bean (*Phaseolus vulgaris* L.) populations under cultivation

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Received 8 July 2002, accepted in revised form 17 April 2003

The objective of this research was to characterise two populations of wild bean grown simultaneously in an experimental field site in Chapingo, Mexico. For comparative purposes, two cultivars of common bean were included. Only seven of 24 phenological and morphological traits (e.g. number of days to emergence, expansion of primary leaves and third trifoliolate leaf, number of branches per plant, diameter of stem, number of flower buds per plant and nodes per branch) investigated were statistically similar between and within wild samples due largely to differences in growth habit. The

number of inflorescences, leaves, pods and seeds per wild plant fluctuated between 72 and 145, 109 and 206, 68 and 284 and 180 and 513, respectively. In contrast, each cultivar was highly homogeneous. Principal component analyses supported the conclusion that these morphological and agronomic characteristics of wild common bean populations primarily depend on the predominant growth habit type and that under different environments, the expression of these traits may change.

Introduction

The genus *Phaseolus* has about 50 species, most of which grow in Mexico (Mercado-Ruaro and Delgado-Salinas 1998), but just five have domesticated variants (Debouck 1999): *P. vulgaris* L., *P. coccineus* L., *P. lunatus* L., *P. acutifolius* L. and *P. polyanthus* L. Of these species, *P. vulgaris* (common bean) is one of the most important crops in the world. It provides the main dietary source of proteins and carbohydrates for large sections of the population (Singh 1999a). Debouck (1999) has stressed the wider range of genetic diversity of wild bean populations — indeed, this diversity should be wider than the domesticated germplasm, because many wild common beans occur between Chihuahua, Mexico (32°N latitude, 110°W longitude) down to Catamarca and Tucuman, Argentine (42°S latitude, 70°W longitude), and from 500m–3 000m altitudes (Toro *et al.* 1990). Cultivated environments are more homogeneous and differ from the environment (both in biotic and abiotic factors) in which the wild common bean grows (Sonnante *et al.* 1994). The wide geographical distribution of the wild populations and their large genetic diversity is accompanied by adaptation to different environments. Hence, along the range of distribution some morphological variation can be observed. Several factors including temperature, humidity, photoperiod and soil fertility in the areas of the ancestral populations must have played an important role in the *in situ*

development of each wild population (Delgado *et al.* 1988, Debouck 1999).

Although some evaluations of wild beans have been carried out, limited evaluation has been done systematically and information about morphological, phenologic and agronomic traits of common bean progenitors under cultivation are scarce. In spite of this, it has been recognised that wild bean germplasm is a promising source for common bean improvement (Debouck 1999, Singh 1999b). As a product of human selection an improved cultivar possesses high morphological, physiological and agronomic uniformity and a reliable degree of stability. In contrast, within wild populations growing *in situ* or under culture, great variability has been observed in growth habits, colour (of flowers, hypocotyl, pod walls and seeds), and pod and seed number (Miranda 1967, Smartt 1988, García *et al.* 1997, Berrocal *et al.* 2002). The wild bean gene pool could be used as a gene source for disease and pest resistance, stress tolerance, and better quality of nutritional and agronomic traits. However, wild beans are not included in breeding programmes because of the limited number of wild accessions in gene banks (Debouck 1999), absence of systematic screening of entire collections and scarce information on morphological, physiological and biochemical characteristics. They may also introduce many undesired traits into cur-

rent breeding material (Smartt 1988, Singh 1999b).

The purpose of the present work was to evaluate the effects of an agronomic environment on the phenological, morphological and agronomic traits of two samples of the wild common bean population from Mexico. This was achieved by growing individuals in an experimental field during four cropping seasons.

Materials and Methods

Biological material and growth conditions

Two samples of wild common bean (*Phaseolus vulgaris* L.) from Mexico, obtained from the germplasm bank of INIFAP (National Institute for Research in Agriculture, Forestry and Animal Husbandry), Mexico, were used (Table 1). Seeds of the wild Durango (WD) population (registered in the Centro Internacional de Agricultura Tropical germplasm bank with the numbers G11033 and DGD-408, according to Toro *et al.* 1990) were collected from plants growing as part of the natural vegetation of the region of origin, 15km south of Tuitán, Saltito, Durango. This is located in the Sierra Madre Occidental and is characterised by a temperate semi-arid climate (García 1988). The wild Tlaxcala (WT) population comes from a temperate humid zone located at La Malinche, Tlaxcala (José A Muruaga M pers. comm., INIFAP, Mex. Mexico). The Bayo Mecentral and Amarillo cultivars were included as controls in the study. The criterion for selecting these cultivars was the colour of the seed coat, cv. Bayo Mecentral and WD are beige, while cv. Amarillo and WT are yellow, 2.5 Y 8/4 and 2.5 Y 7/10, respectively (according to the Munsell Colour Charts for Plant Tissues, Anonymous undated). The cultivars Bayo Mecentral and Amarillo were developed in the INIFAP experimental station at Chapingo. Both cultivars have growth habit III (prostrate).

This study was carried out over four consecutive cropping seasons in an experimental field of the Colegio de Postgraduados, in Chapingo, Mexico (Table 1). Monthly temperature and precipitation for the cropping seasons are presented in Figure 1. The plot for each wild sample and cultivar consisted of twelve 8m rows spaced 75cm apart. Thirty-five days after sowing (DAS), when the third trifoliolate leaf was completely unfolded in 50% of the plants, each plant was observed every 15 days to identify its growth habit and to describe the phenology. Sub-samples or sub-populations were represented by plants grouped according to each main growth habit registered in both wild samples. The experimental unit was a randomly chosen plant and eight plants of each sub-sample and cultivar were evaluated at each sam-

pling date. Seeds from the wild original samples were used in the first and the fourth cropping seasons, whereas the previous season's crop was the seed source in the second and the third cropping seasons.

Plant structure and phenology

In order to evaluate plant morphology, eight samplings were performed at intervals of 15 days from 35 DAS until harvest. Harvest was carried out at physiological maturity, when at least 95% of the pods in each sub-sample had the characteristic yellow-brown colour, according to Nienhuis and Singh (1986). To identify each growth stage and to select morphological attributes, the conventional descriptions for *Phaseolus* were used (Singh 1982, CIAT 1987), as follows: (1) number of branch inflorescences, (2) number of branches per plant (number of stem branches with at least one node), (3) diameter of stem (cm) (measured at the base of the second internode from the ground), (4) length of stem (cm) (the distance from the cotyledonary node to the node of the last fully expanded trifoliolate leaf), (5) length of stem internode (cm) (the stem length divided by the number of nodes on the stem), (6) number of stem inflorescences, (7) number of stem nodes (all the stem nodes from the cotyledonary node to the node of the last trifoliolate leaf), (8) number of nodes per plant (the total number of stem nodes plus the nodes of the branches), (9) number of pods per plant, (10) number of seeds per plant, (11) leaf number and (12) leaf area.

Data analysis

An analysis of variance (ANOVA) was performed on each group of variables and the multiple comparisons of means for the main resulting habits by Tukey's test, according to a completely randomised design. Multivariate analysis (principal components) was also performed. The statistical analysis was performed including the maximum values of each trait. Also, the models of curvilinear regression with the best adjustment to the growth kinetics and development of the vegetative and reproductive organs were chosen. All statistical analyses were performed with the statistical package SAS for PC (SAS Institute 1985).

Results

Growth habits

The growth habits of the four recognised common beans

Table 1: Location, climate and mean annual rainfall from origin site of two wild common bean samples, and location and climate of experimental site of wild and domesticated common bean

Wild sample	Location	Climate, precipitation and annual mean temperature*
Durango (WD)	Saltito, Durango, (23°58'N, 104°18'W)	BS ₁ kw(w)(e), 1 820m asl and 17.7°C
Tlaxcala (WT)	La Malinche, Tlaxcala, (19°25'N, 98°8'W)	Cw ₂ (w)(i)g, 2 404m asl and 15°C
Cultivars	Experimental site	
Amarillo, Bayo Mex	Chapingo, Mexico, (19°29'N, 98°53'W)	Cw(i)g, 2 240m asl and 15°C

* According to García (1988)

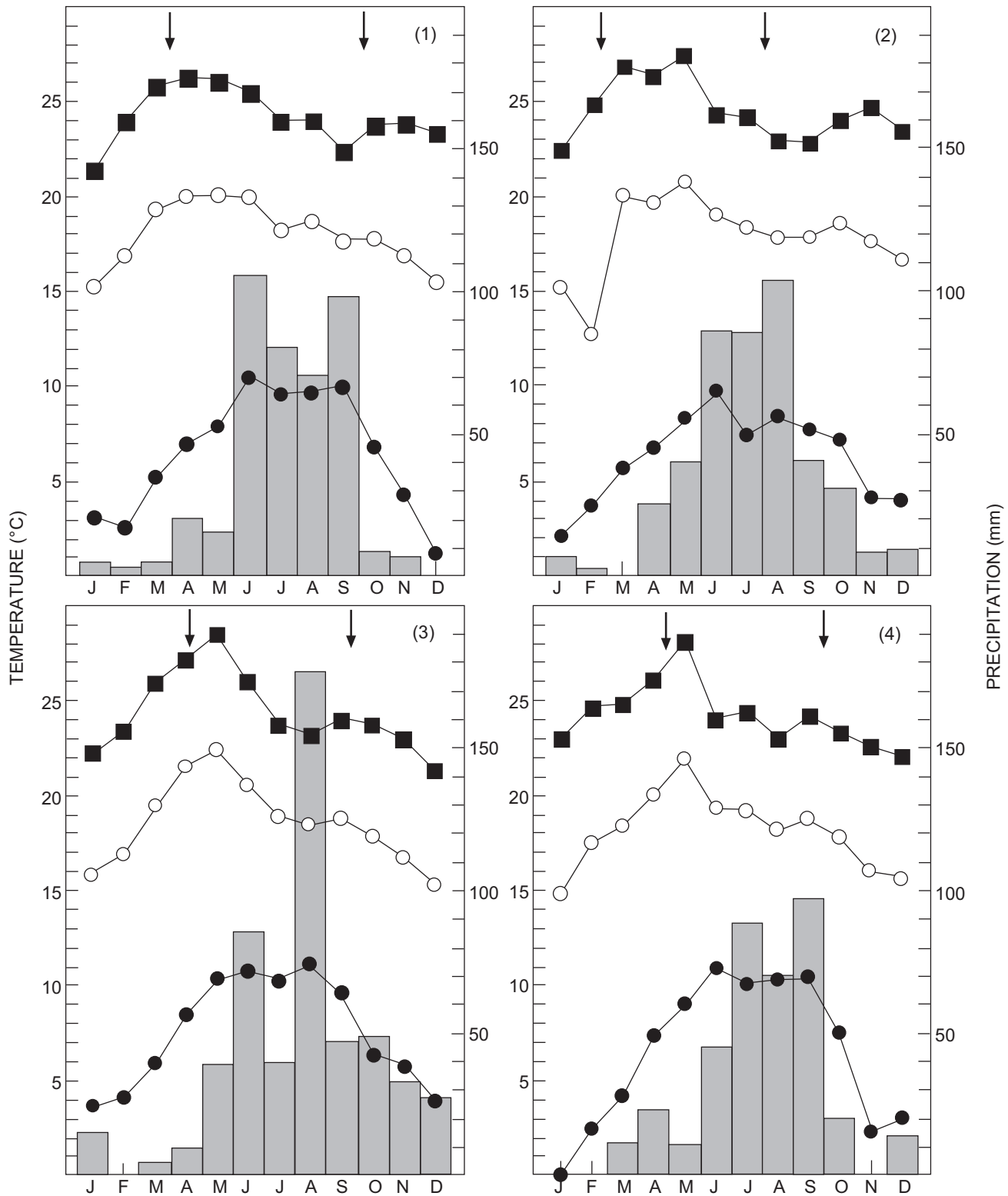


Figure 1: Climographs for the experimental period. Minimum (●), mean (○) and maximum (■) monthly mean temperature. Arrows at the top indicate sowing and harvest date, respectively (Data source: Meteorological Observatory of Universidad Autónoma Chapingo)

were present in both wild samples in the four cropping seasons. The proportion of growth habits fluctuated among and within wild samples. In general, habit I (determinate growth-habit and bushy type with stem and branches terminating in a reproductive bud) and habit III (indeterminate growth-habit and semiclimber with terminal vegetative meristem) were scarce or absent in both wild samples; in contrast, growth habits II and IV (stem and branches topped by a vegetative meristem, climbing) were recorded in all cropping seasons, but their relative proportions fluctuated between 24% and 91% (habit II) and between 9% and 53% (habit IV) in both samples. The heterogeneity in proportion of growth habits in wild bean sharply contrasted with the homogeneity in the domesticated common bean. In both cultivars all plants had indeterminate growth habit III (Table 2).

Morphological and phenological differences of wild plants in response to cultivation were more evident in the growing season when bushy type plants were present. For the most conspicuous morphological characteristics a gradient between growth habits was observed, where plants of growth habit I were far apart from habit IV. Plants with growth habit I presented bush-like growth and a determinate growth habit (stem and lateral branches terminating in a reproductive bud), with a short stem and few branches per plant. Plants with growth habit IV showed an indeterminate growth habit with climbing capacity, profuse branching in a long stem and profuse foliage.

In order to quantify the apparent variability, a characterisation of the stage of growth and development of the four growth habits in wild plants was necessary. However, each growth habit was not always present, or it was in a low proportion (Table 2). For these reasons in the next part of this paper only results from the second cropping season are presented. In this case 91% of the 115 plants of WD sample had growth habit II (WDII) and 45% and 50% of the 107 plants of the WT sample had growth habit II (WTII) and IV (WTIV), respective-

ly (Table 2). Thus only, the WDII, WTII and WTIV sub-samples had sufficient experimental units for sound statistical analysis.

Growth and development stages

Based on the suggested criteria for the description of the growth stages of bean cultivars (Fernández *et al.* 1983), it was determined that the duration of the vegetative and reproductive stages in WDII sub-sample was quite similar to WTII, on average, 52 days for the vegetative stage and 123 days for the reproductive stage. However, there were significant differences in the time required to develop the first trifoliolate leaf, time to flowering, duration of flowering, time to pod growth and time to reach physiological maturity. The WTII sub-sample, originally from a temperate humid region and at a higher altitude than WDII, was precocious in reaching these physiological stages. In contrast to growth habit II sub-samples, the vegetative and reproductive stages of the WTIV sub-sample were extended up to 63 days and 159 days, respectively. On average both cultivars required six days to start flowering, but cv. Bayo Mecentral reached physiological maturity almost 10 days before cv. Amarillo (Table 3).

According to some traits of indeterminate growth habit, the three sub-samples continued developing vegetative structures after the reproductive stage had started. The period of overlap was similar in the three sub-samples and extended up to 110–115 DAS. The main differences regarding precocity between the three sub-samples were observed in the reproductive stage. The WDII and WTII sub-samples required on average 11 days less than the WTIV sub-sample to start flowering, but differences in time to reach the next phenological stages were increasing in the WTIV sub-sample which reached physiological maturity 35 days after WDII and WTII sub-samples (Table 3).

Although all vegetative and reproductive plant structures in

Table 2: Growth habits for two wild *Phaseolus vulgaris* L. samples and two cultivars grown in Chapingo, Mexico

Growth habit**	Cropping season	Number of plants							
		Wild from Durango		Wild from Tlaxcala		Cv. Bayo Mecentral		Cv. Amarillo	
		Absolute	Relative (%)	Absolute	Relative (%)	Absolute	Relative (%)	Absolute	Relative (%)
I	1993	4	7.4	3	6.5	0	0.0	0	0.0
	1994	0	0.0	6	6.0	0	0.0	0	0.0
	1995	9	12.2	0	0.0	0	0.0	0	0.0
	1996	0	0.0	32	64.0	0	0.0	0	0.0
II	1993	32	59.3	27	58.7	0	0.0	0	0.0
	1994	105	91.0	48	45.0	0	0.0	0	0.0
	1995	27	36.5	43	66.2	0	0.0	0	0.0
	1996	12	40.0	12	24.0	0	0.0	0	0.0
III	1993	0	0.0	3	6.5	107	100.0	103	100.0
	1994	0	0.0	0	0.0	105	100.0	109	100.0
	1995	0	0.0	0	0.0	148	100.0	101	100.0
	1996	2	6.7	0	0.0	109	100.0	105	100.0
IV	1993	18	33.3	13	28.3	0	0.0	0	0.0
	1994	13	9.0	52	50.0	0	0.0	0	0.0
	1995	38	51.4	22	33.9	0	0.0	0	0.0
	1996	16	53.3	6	12.0	0	0.0	0	0.0

** Growth habit I: bushy determinate; habit II: bushy indeterminate; habit III: prostrate indeterminate; and habit IV: climbing indeterminate (García *et al.* 1997)

Table 3: Phenology of the predominant growth habits in two wild *Phaseolus vulgaris* L. samples and two cultivars grown in Chapingo, Mexico

Growth stage (Days to)	Sub-sample*				Cultivar		
	WDII	WTII	WTIV	CV	Bayo Mecentral	Amarillo	CV
Emergence	10.9a	10.0a	11.0a	7.88	9.8a	10.8a	5.65
Primary leaves	13.0a	12.7a	13.0a	5.26	12.0a	12.1a	5.42
First trifoliolate leaf	18.2a	16.5c	17.2ab	3.63	19.2a	17.5b	2.66
Third trifoliolate leaf	29.4a	28.0a	29.5a	4.06	27.0b	29.5a	2.09
Start flowering	53.0b	51.2b	63.2a	4.73	61.0a	62.5a	1.21
Flowering (duration of)	69.4b	63.5c	78.5a	5.07	73.8b	77.3a	1.01
Pod wall growth	81.5b	75.5c	90.2a	3.94	88.8a	88.8a	0.46
Pod filling	106.2b	101.2b	126.5a	5.48	122.2b	126.2a	0.91
Physiological maturity	128.5b	127.5c	158.5a	5.53	143.0a	152.5a	0.54

* WDII: plants with growth habit II from Saltito, Durango, Mexico. WTII and WTIV plants with growth habit II and IV, respectively, from La Malinche, Tlaxcala, Mexico. Values followed by the same letter within a row are not different at the P = 0.05 level of Tukey's test

the three wild sub-samples increased according to a cubic polynomial trend ($y = \beta_0 + \beta_1x + \beta_2x^2 + \beta_3x^3$), differences in the time to reach the maximum values in some of these structures were observed between sub-samples. Thus, the WTIV sub-sample continued increasing its foliage until 110 DAS and WTII and WDII sub-samples reached their maxima about 15 days later. Number of pods and seeds continued increasing until 140 DAS and 160 DAS in WDII sub-sample, but both sub-samples from Tlaxcala reached the maximum number of these organs 15 days later (Figures 2 and 3, Table 4). In contrast to wild common bean the stem growth, branch exposition, pod and seed accumulation in domesticated common bean followed a quadratic trend ($y = \beta_0 + \beta_1x + \beta_2x^2$), also the domesticated plants developed synchronically (Figures 2 and 3).

Vegetative and reproductive structures

As expected, most morphological traits of the growth habit IV sub-sample showed significant differences from those of habit II; only the length of stem and the number of nodes in the stem were significantly different between sub-samples with habit II. The WTIV plants, apart from being the tallest, also seemed stronger, since they had longer internodes and more nodes per plant, a greater leaf area per plant, and a greater number of leaves than in growth habit II plants (Table 4). However, the similarity of the mean leaf size of the WTII and WTIV sub-samples (0.38dm² and 0.35dm², respectively), as well as the smaller mean leaf size of the WDII sub-sample (0.27dm², Figure 2), was striking. The number of reproductive structures (inflorescences per branch and stem, flower buds, pods and seeds per plant) was statistically similar between both growth habit II sub-samples, but was significantly smaller than in the growth habit IV plants (Table 4).

Although there were few plants with growth habit I in wild samples from Tlaxcala (WTI) and habit IV in the sample from Durango (WDIV) from which to evaluate growth kinetic trends, the mean value of some morphological traits was obtained at harvest (Table 4). Length of stem, nodes per branch and in the stem, and number of nodes, pods and seeds per plant in WTI sub-sample tended to be less than 25% of WTIV (Table 4).

Although both cultivars had growth habit III, cv. Amarillo was significantly taller than cv. Bayo Mecentral, and had double the number of seeds per plant. The value for other plant structures like leaves, branches and pods per plant were similar (Table 4).

Multivariate analysis

A global morpho-phenological pattern in the WDII, WTII and WTIV sub-samples and in both cultivars was revealed by the principal component (PC) analysis. In the case of wild plants, for the 24 morphological and phenological variables evaluated the first three PC accounted for 50% of the total variability (Table 5). When the first PC (PC1) was plotted against the second PC (PC2) and the latter one against the third PC (PC3), a certain overlap was observed between sub-samples with growth habit II (WDII and WTII), regardless of their geographic origin. Additionally, WTIV sub-sample was clearly separated from WDII and WTII along the PC2, and the samples were arranged almost linearly along PC1. The major separation between habit II and IV plants was caused by the main variables that made up PC2 (Figure 4a–c). In part, as a result of a greater dispersion of the two growth habit II sub-samples, the overlap between the three wild sub-samples increased in the ordination configured by PC3 and PC1. However, both habit II sub-samples remained at the extremes of PC1, with only a small overlapping region, indicating that they could be considered as different biological entities. Even though the WTIV sub-sample was located between WDII and WTII, it remained ordered along the PC1 (Figure 4b). In the case of the cultivars, the first three PC accounted for 80.6% of the total variability (Table 5) and the separation of cv. Bayo Mecentral from Amarillo in the PC plot was caused mainly by PC1 (Figure 5a–c). The most important variables contributing to CP1 included 14 (six phenological and eight structural) traits (Table 6).

Discussion

Differences in phenological traits of wild common bean, such as duration of flowering, time to pod wall growth and to physiological maturity (Table 2) could be, in part, a response to the environment of cultivation. The WD sample comes from

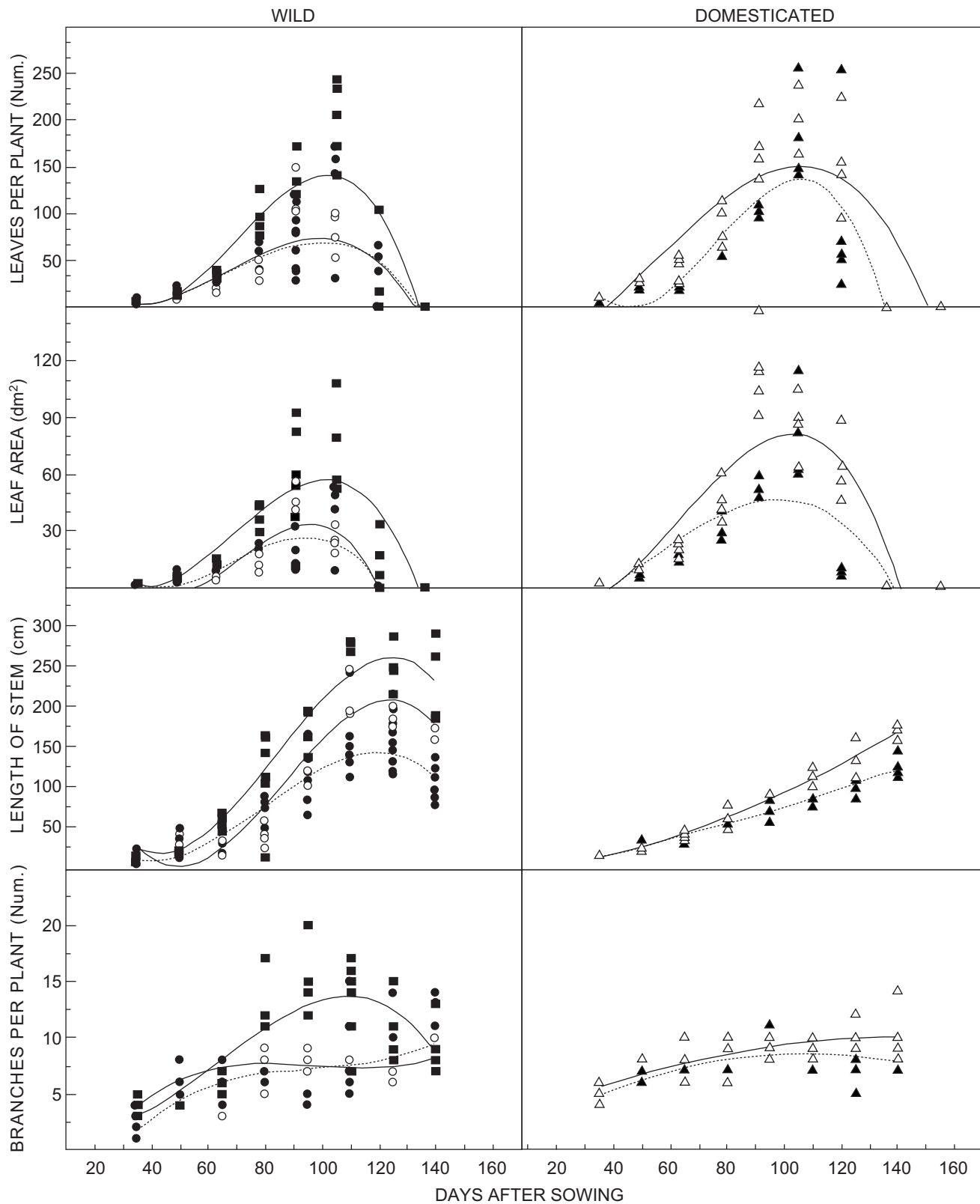


Figure 2: Leaves per plant, leaf area, length of stem and branches per plant of the predominant growth habits in two wild *Phaseolus vulgaris* L. samples and two cultivars cultivated in Chapingo, Mexico (Wild sub-samples: (●) WDII: plants with growth habit II from Saltito, Durango, (○) WTII and (■) WTIV plants with growth habit II and IV from Tlaxcala; cultivars: (▲) Bayo Mecentral and (△) Amarillo)

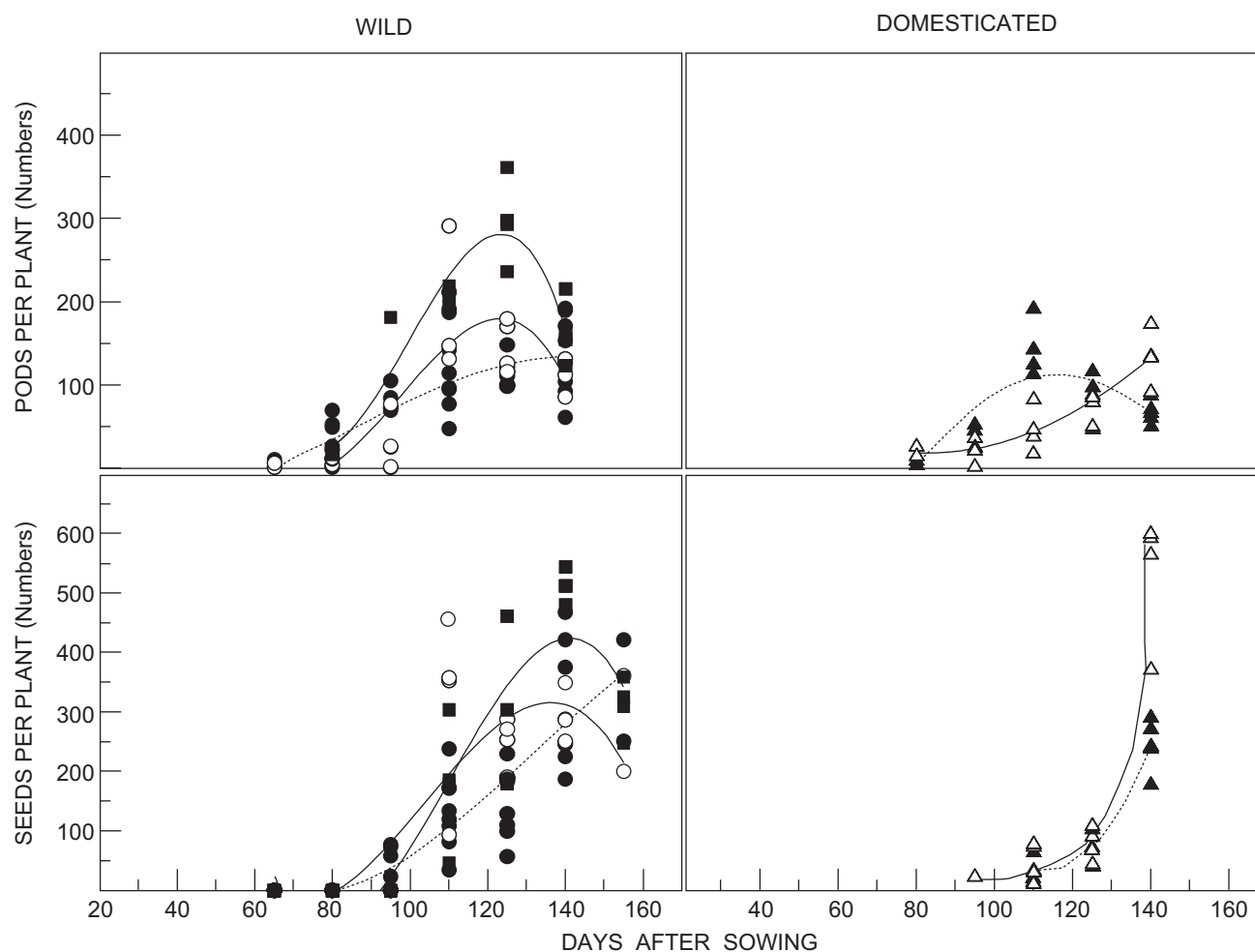


Figure 3: Pods and seeds per plant of the predominant growth habits in two wild *Phaseolus vulgaris* L. samples and two cultivars cultivated in Chapingo, Mexico (Wild sub-samples: (●) WDII: plants with growth habit II from Saltito, Durango, (○) WTII and (■) WTIV plants with growth habit II and IV from Tlaxcala; cultivars: (▲) Bayo Mecentral and (△) Amarillo)

a semi-arid zone in northern Mexico and, at least for bean cultivars, this zone is more suitable for the bushy or the short cycle prostrate variants (i.e. habits II and III) (Singh 1989). Remarkably, in the present study WD samples produced plants with habit III only in one growing season and in a very small proportion (6.7%) (Table 2). In contrast, the temperate humid region at higher altitude with a more profuse vegetation and lower evapo-transpiration demand seems to be more suited for the genotypes with habit IV, i.e. indeterminate, late maturing and climbing forms (Singh 1999c). In other samples of the same wild population from Durango included in the present study, but cultivated in a greenhouse, García *et al.* (1997) and Berrocal *et al.* (2002) obtained 82% and 96% of indeterminate growth habit (II, III and IV) and 96% (IV), and the remaining 18% and 4% determinate-bushy growth corresponding to habit I, respectively. Therefore, it seems that the cultivation environment modulates the expression and frequency of growth habits in the surviving individuals of a wild bean sample. Such a response to the environment was observed in nine and four cultivars of a group of 249 common bean accessions, which

expressed determinate and indeterminate growth habits, respectively, when cultivated in Cali, Colombia, but they had the opposite growth habit in Cambridge, United Kingdom (Vanderborcht 1988). Similarly, in open ground wild *P. polyanthus* covered the soil before climbing, but plants climbed immediately under greenhouse cultivation (Smartt, 1969). However, variation in temperature or precipitation between growing seasons was not totally responsible for the wide differences in morphological traits between and within WD and WT samples. Minimum, mean, and maximum temperature (T_{\min} , T_{mean} , and T_{\max} , respectively) fluctuated generally in a similar way and reached similar values during each developmental stage during every growing season. Mean temperature in all four growing seasons fluctuated between 19°C and 22°C (Figure 1). During emergence, and on some occasions up to the appearance of the primary leaf, water was supplied twice weekly because precipitation was scarce (Figure 1).

It is unlikely that hybridisation between different wild populations was a cause of variation in growth habits, since according to Stoetzer (1984) and Triana *et al.* (1993) wild *P.*

Table 4: Morphologic and agronomic traits of the predominant growth habits in two wild *Phaseolus vulgaris* L. samples and two cultivars, grown in Chapingo, Mexico

Traits	Sub-sample*						Cultivars		
	WDII (n = 8)	WDIV (n = 7)	WTI (n = 4)	WTII (n = 8)	WTIV (n = 8)	CV	Bayo Mecentral (n = 8)	Amarillo (n = 8)	CV
Branch inflorescence (no.)	59.5b	–	–	52.3b	109.5a	103.74	9.8a	5.3a	58.49
Diameter of stem (cm)	0.2a	0.4	0.4	0.2a	0.3a	28.80	0.2a	0.2a	14.57
Flower buds per plant (no.)	62.1a	–	–	48.4a	65.0a	231.36	70.8a	32.5b	37.81
Inflorescence per plant (no.)	72.4b	–	–	73.5b	145.0a	218.20	111.2a	106.5a	25.31
Leaf area (dm ²)	29.7b	–	–	45.1b	71.7a	11.99	81.9a	86.1a	24.66
Leaves per plant (no.)	108.5b	–	–	118.6b	205.5a	109.60	181.3a	206.a	23.71
Length of stem (cm)	150.0c	261.1	58.3	217.0b	267.0a	73.48	119.5b	164.8a	8.10
Nodes per branch (no.)	11.4a	19.7	3.8	11.5a	15.5a	87.41	27.0b	37.8a	24.20
Nodes per plant (no.)	146.5b	391.9	38.2	124.4b	261.8a	94.42	252.8b	411.3a	23.04
Pods per plant (no.)	136.6b	141.8	67.8	195.0b	284.2a	131.13	142.3a	132.8a	24.82
Seeds per plant (no.)	307.6b	369.8	179.5	341.0b	512.5a	169.02	237.3b	544.8a	23.31
Stem branches (no.)	9.9a	18.8	9.2	8.4a	15.2a	38.74	9.3a	10.3a	23.50
Stem inflorescence (no.)	12.8b	–	–	21.3ab	35.5a	123.67	5.5a	3.0a	41.87
Stem internode length (cm)	6.3b	10.6	8.4	7.4b	9.0a	48.93	5.4b	6.4a	7.99
Stem nodes (no.)	24.1b	24.8	7.3	29.1a	30.0a	43.36	22.5a	26.0a	12.93

* Values followed by the same letter within a row are not different at the P = 0.05 level of Tukey's test. Plants from Durango (WD) or Tlaxcala (WT), with growth habit I, II or IV

Table 5: Eigenvalues and proportion of the variance explained for the first three principal components, generated from different groups of morphological, phenological and agronomic traits of wild and domesticated common bean samples and two cultivars

Principal component	Eigenvalue	Proportion of variance explained	
		Individual	Cumulative
Wild common bean	Twenty four variables		
1	4.718	0.197	0.197
2	4.345	0.181	0.378
3	2.818	0.117	0.495
	Eighteen variables		
1	4.536	0.252	0.252
2	3.703	0.206	0.458
3	2.558	0.142	0.600
Domesticated common bean	Twenty three variables		
1	12.180	0.529	0.529
2	4.250	0.184	0.714
3	2.109	0.091	0.806

vulgaris tends to be self-pollinated and natural cross-fertilisation among populations is not significant. Nevertheless, Gepts and Debouck (1991) and Ibarra-Perez *et al.* (1997) stressed that spontaneous crossing, or natural hybridisation, in both wild and domesticated common bean is not rare, and depends on the environment, its location, the specific genotype and the availability of pollinating insects. Although in the present work the variability in growth habits in wild bean was confirmed it seems necessary to evaluate the real outcrossing rate in these wild common bean populations.

The characteristics of the WTIV sub-population, namely profuse branching, long internodes (10–20cm), high number of nodes (262 per plant) and continuous growth of the main axis (2–5m), have been considered as typical of wild bean (Gepts and Debouck 1991). It could be accepted that the experimental environment altered the relative frequency of growth habits expressed by the WT sample (three of the four main types), because it was different from that of the original

region. It is worth pointing out that in the bean cultivars the differences in the phenotypic expression of growth habit are genetically controlled by: (a) type of growth of the terminal bud (vegetative or indeterminate vs. reproductive or determinate), (b) thickness and resistance of the stem (strong vs. weak) and stem internode length, (c) climbing capacity and presence or lack of prostrate branches and (d) distribution of pod load at the base, along the entire length, or largely in the upper portion of the plant (Singh 1989, Koenig and Gepts 1989). Besides, some traits associated with growth habit, such as number and length of branches, thickness of stem, climbing or creeping capacity, nodes per plant and stem nodes, are also strongly affected by the environment in bean cultivars (Adams 1982). In the present work, the heterogeneity of growth habit in the wild common bean samples contrasted with the homogeneity in domesticated common bean, since, as it was expected, both cultivars had plants with growth habit III only.

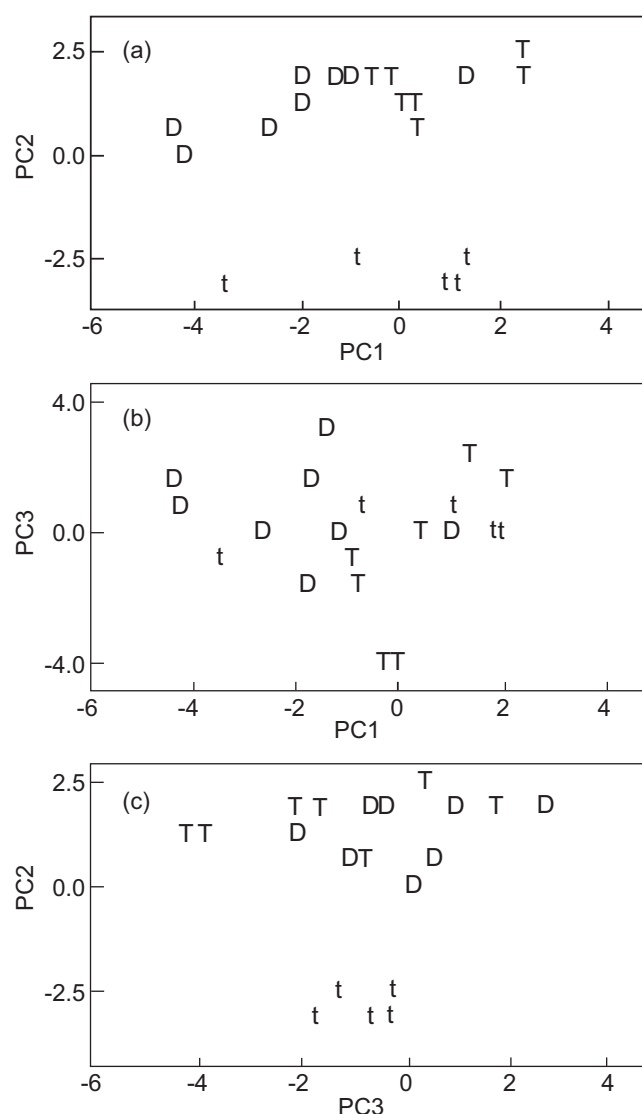


Figure 4: Ordination on the first three axes or principal components (PC) (a: PC 1 and 2; b: PC 1 and 3; and c: PC 2 and 3) of the experimental units of two wild *Phaseolus vulgaris* L. samples, cultivated in Chapingo, Mexico, based on 24 morphological and phenological traits (D: plants with growth habit II from Durango; T and t: plants with growth habit II and IV, respectively, from Tlaxcala)

As far as growth pattern according to the habits is concerned, the development of all plant structures, namely leaves (number and area per plant), stem (length) and branches (number per plant), as well as reproductive organs (number of pods and seeds per plant), in WDII, WTII and WTIV sub-samples, followed a cubic polynomial trend through time ($y = \beta_0 + \beta_1x + \beta_2x^2 + \beta_3x^3$; Figures 2 and 3). These results indicate that the growth pattern of both vegetative and reproductive organs in wild common bean plants is similar between growth habits independent of geographical origin. However, differences in the growth rate, mainly leaf area, appear to affect C assimilation over the whole growth season, as well as source-sink relationships during reproduction (Nienhuis and Singh 1985). It has also been

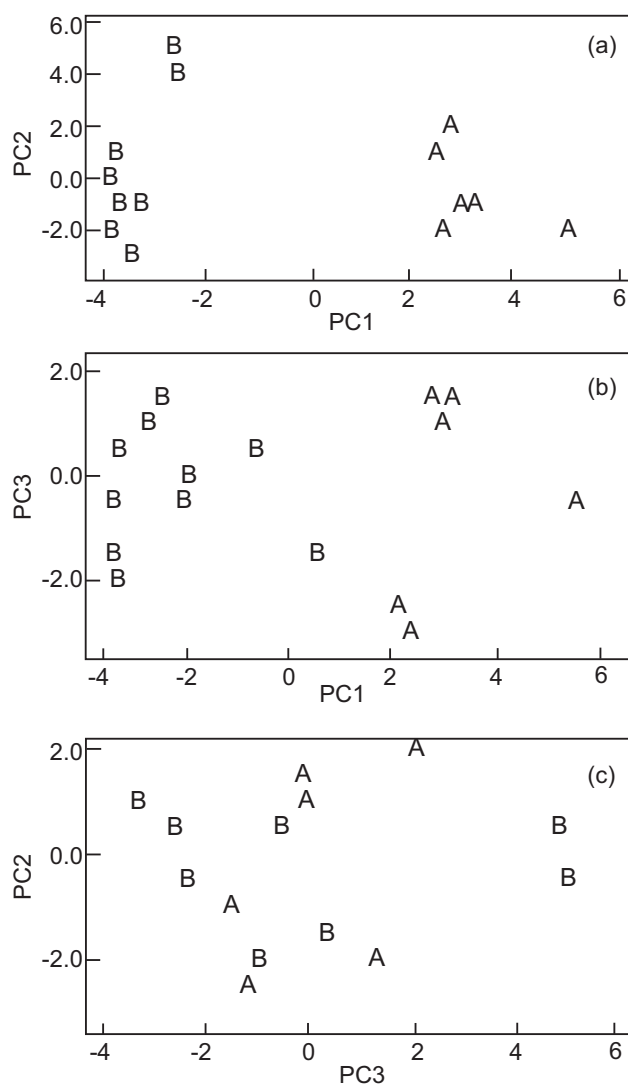


Figure 5: Ordination on the first three axes or principal components (PC) (a: PC 1 and 2; b: PC 1 and 3; and c: PC 2 and 3) of the experimental units of two *Phaseolus vulgaris* L. cultivars, cultivated in Chapingo, Mexico, based on 23 morphological and phenological traits (A: cv. Amarillo and B: cv. Bayo Mecentral)

observed that an accelerated natural defoliation, due to leaf senescence during pod filling, reduces the leaf area efficiency of wild plants (Berrocal *et al.* 2002). Differences in the source-sink relationships during the reproductive stage between and within wild and domesticated variants could be responsible for contrasts in yield components (Table 4). Effects of the domestication process on plant growth and development of common beans were indicated by the different growing trends of the vegetative (stem and number of branches per plant) (Figure 2) and reproductive (number of pods and seeds per plant) structures (Figure 3).

Vegetative structures (leaves, branches and stem) of wild common bean reached maximum development after 95 DAS to 110 DAS, when pods and seeds were actively grow-

Table 6: Eigenvectors for the first three principal components (PC), generated from morphological, phenological and agronomic traits of two wild common bean samples and two cultivars

Trait	Wild samples			Cultivars		
	PC1	PC2	PC3	PC1	PC2	PC3
Branch inflorescence (no.)	0.078	-0.215	-0.337	-0.244	0.000	-0.243
Diameter of stem (cm)	0.178	0.128	-0.062	-0.092	-0.291	0.426
Duration of flowering (days)	-0.055	0.432	0.028	0.064	0.152	0.359
Emergence (days to)	-0.343	-0.223	-0.003	0.118	-0.305	-0.223
First trifoliolate leaf (days to)	-0.352	-0.060	0.139	-0.253	-0.027	0.227
Inflorescences per plant (no.)	0.092	-0.183	0.222	-0.222	0.163	0.283
Leaf area (dm ²)	0.331	-0.000	0.159	0.124	0.278	-0.138
Leaves per plant (no.)	0.003	0.150	0.279	0.263	0.121	-0.069
Length of the stem (cm)	0.127	0.305	-0.113	0.275	-0.032	-0.138
Nodes per branch (no.)	-0.144	-0.152	-0.084	0.245	0.188	0.047
Nodes per plant (no.)	0.167	0.197	0.217	-0.029	0.289	0.451
Physiological maturity (days to)	0.296	-0.110	0.029	0.216	-0.211	-0.095
Pod filling (days to)	0.203	-0.294	-0.354	0.281	-0.056	0.016
Pod wall growth (days to)	0.039	0.241	-0.169	0.256	-0.167	0.066
Pods per plant (no.)	0.019	0.162	0.299	0.262	-0.059	0.221
Primary leaves (days to)	0.332	0.157	-0.045	-0.253	-0.027	0.227
Reproductive buds per plant (no.)	0.172	0.122	-0.053	-0.222	0.163	0.283
Seeds per plant (no.)	-0.132	0.015	-0.359	0.189	0.321	-0.137
Start flowering (days to)	0.230	-0.294	0.089	-	-	-
Stem branches (no.)	-0.039	-0.077	0.169	0.071	0.380	0.190
Stem inflorescences (no.)	-0.053	-0.175	0.206	0.238	-0.117	-0.129
Stem internode length (cm)	-0.246	0.210	-0.345	0.144	0.265	0.020
Stem nodes (v)	0.098	-0.311	0.124	0.264	-0.137	0.162
Third trifoliolate leaf (days to)	-0.345	0.030	0.231	0.217	-0.224	0.171

ing, resulting in competition between vegetative and reproductive organs during the reproductive stage. In contrast, vegetative structures in domesticated common bean had reached their maximum growth when pods and seeds started to grow (Figures 2 and 3). Similar growth patterns were observed by a comparison between a wild common bean and a cultivar growing under greenhouse conditions (Berrocal *et al.* 2002).

When wild samples were grown together in a different climate from their places of origin, the growth rate of the leaf surface in the habit II sub-population from the temperate humid region (WTII) was higher (it peaked at 95 DAS) than that of both the habit IV from the same sample (WTIV) and habit II from the semi-arid region of northern Mexico (WDII) (Figure 2). In contrast to the homogeneity during vegetative growth, the wild bean showed great variability during the reproductive growth stage (Table 3). As with the cultivars (Gepts 1987), the time to reach flowering, pod development, seed development and maturity were different between samples from different regions and sub-samples (Table 3). Based on the time required to start flowering and for peak flowering, sub-populations with growth habit II were more precocious than those with growth habit IV (Table 3). According to Voysest and Dessert (1991), independent of the time required to reach physiological maturity (from 70–300 days), cultivars are classified from early to late cultivars; those of bushy and semi-climbing growth habit II and some of habit III are precocious, and those with a long climbing stem and branches (habits III and IV) are late. Since duration of the growth stages of bean cultivars depends strongly on climatic factors, especially light and temperature, plants

with growth habit II and III require between 90–120 days to mature in temperate humid climates, whilst those of growth habit IV require between 120–150 days. However, this period can be reduced, according to the growth habit, to between 75–120 days in warm climates (CIAT 1987). The effect induced by warmer environments in a greenhouse (30°C/15°C of mean day/night temperatures) could explain the shorter time (80–108d) required to reach physiological maturity, observed previously in other WD samples (Berrocal *et al.* 2002, García *et al.* 1997), which contrasts with the 128d in the present work (25°C/11°C) (Table 3 and Figure 1). An increase in time to the end of vegetative and reproductive stages for the cv. Bayo Mecentral was observed (11 days and 35 days, respectively) in the present work, similar to that seen by García *et al.* (1997), when plants were grown in a greenhouse. Our results are consistent with other studies on the effects of environment on the expression of phenological, morphological and physiological traits in wild variants (Lynch *et al.* 1992), landraces or traditional cultivars (Singh *et al.* 1996) and improved cultivars (Singh *et al.* 1991).

Multivariable analysis of the wild sub-samples indicated that the six most important variables contributing to PC1 were leaf area and days to emergence, presence of primary leaves, first and third trifoliolate leaves and time to physiological maturity. The five most important variables contributing to the PC2 were stem nodes and length, number of days to start flowering, duration of flowering and days to pod fill. The six most important variables contributing to the PC3 were branch inflorescences, stem internode length, days to pod fill and leaves, pods and seeds per plant (Table 6). It

should be stressed that a second analysis of PC was carried out without the six variables (days to start the pod filling period was important in more than one PC). In contrast, the number of branches, inflorescences and flower buds per plant, diameter of the stem, nodes per branch and days for pod wall growth made a small contribution, but the proportion of the variance explained by the first three components was only slightly increased (Table 5). Principal Component 1 was mainly made up of variables associated with establishment and overall precocity. This explains the separated array of the WDII and WTII sub-samples on this axis or component, since the sub-population from Tlaxcala was generally more precocious (Table 4). The PC2 separated clearly the WTIV sub-population from WTII and WDII, since the most important variables of PC2 were related to the climbing ability of the stem and to the length of the life cycle (Table 3 and 6). Finally, the PC3 was a gradient of profusion of organs (leaves, inflorescences and seeds) with their concomitant structures, which determined the closer array of both sub-populations from Tlaxcala (WTII and WTIV) (Tables 2 and 3). Separation of one cultivar from the other in the PC plots was caused mainly by the PC1 (Figure 5a–c), in this case more than a half of the variables included in the PC analysis were associated with the CP1 (six phenological and eight structural traits) (Table 6). Differences in the variables with relatively high weight in each CP, between the wild sub-samples and the cultivars could be taken as part of the domestication syndrome, which has been defined as a suite of traits distinguishing cultivars and wild bean plants (Gepts 1999). Phenology is included amongst these traits.

The samples evaluated in this study are from climatically very different geographical regions, namely temperate, semi-arid (Saltito, Durango) and temperate, almost humid (La Malinche, Tlaxcala). In particular, the presence of humidity and the fluctuation of environmental temperature prevailing in these regions (Table 1) could be selective factors determining the frequency and expression of habits and characteristic growth stages for each population. Also, the wide geographical origin of the wild populations suggest a distinct genetic variability.

Information on the composition, phenology and frequencies of the growth habits in wild bean stands in their original habitats is limited. In the wild they would probably show all the known growth habits, although in different proportions from those registered in the present work. That environmental conditions may modulate the expression of the growth habit and the phenology, at least under cultivation, is supported by comparing the results obtained for the same WD population, under greenhouse conditions (Berrocal *et al.* 2002, García *et al.* 1997), with those of this study. Under greenhouse conditions (García *et al.* 1997), the plants of habit II were, on average, 100cm shorter, with fewer nodes in the stem, eight times less pods, and flowering and maturation several weeks before the plants grown in the experimental field.

All these results indicate that differences in phenotypic expression of growth habits, morpho-physiological and agronomic attributes in wild beans partially depend on the original habitat. More specifically, they may depend on the climatic conditions of the geographical region of origin. Under

cultivation, climatic conditions will be very different and will influence development significantly. At present, there is insufficient evidence to determine the environmental components that regulate the morphology of common wild beans.

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