Variation in parameters related to growth in six genotypes of determinate shrub and indeterminate prostrated beans (*Phaseolus vulgaris* L.)

Variación en parámetros relacionados con el crecimiento de seis genotipos de fríjol arbustivo e indeterminado postrado (*Phaseolus vulgaris* L.)

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ABSTRACT

A group of six common bean accessions of the Mesoamericano and Andino genetic groups of the Colombia national germplasm bank at the Corporación Colombiana de Investigación Agropecuaria (Corpoica) was evaluated using 41 quantitatives. The results revealed that five components explained 70.33% of the total variability of the six accessions and 13 variable were selected that were essential for differentiating the variation, including: dry weight of primary leaves, dry weight of trifoliate leaves, pod dry weight, seed dry weight, number of leaves, leaf area ratio (LAR), relative growth rate (RGR) and leaf temperature. Of the two groups of cultivars, the three Meso-American ones were less efficient in the translocation of assimilates than the Andean ones because they had a higher number of leaves and, even with a high LAR, seen as the ratio of assimilation material per unit of plant material, they did not present the higher RGR values on average. Specifically, the Meso-American cultivar Tolima 16, which presented a relatively high seed dry weight, and the Andean cultivars Mexico 497 and Antioquia 19, which had a relatively low number of leaves, presented a high pod dry weight and so were highly efficient.

Key words: Growth analysis, plant physiology, growth habit, evaluation.

RESUMEN

Mediante el empleo de 41 caracteres cuantitativos de tipo fisiológico se evaluó un grupo de seis accesiones de fríjol arbustivo de los acervos genéticos Mesoamericano y Andino del banco de germoplasma de la nación colombiano ubicado en la Corporación Colombiana de Investigación Agropecuaria (Corpoica). Los resultados mostraron que cinco componentes explican el 70,33% de la variabilidad de las seis accesiones y se seleccionaron 13 variables de importancia en la discriminación varietal, entre las cuales sobresalen: peso seco de hojas primarias, peso seco de hojas trifolioladas, peso seco de las vainas, peso seco de semillas, número de hojas, relación área foliar (RAF), la tasa de crecimiento relativo (TCR) y la temperatura de la hoja. De los dos grupos de cultivares se tiene que los tres mesoamericanos son menos eficientes en la traslocación de asimilados que los andinos ya que presenta un número superior de hojas y aun cuando presentan una mayor RAF entendida como la relación del material asimilatorio por unidad de material de la planta no muestran en promedio los mayores valores de la TCR. Específicamente el cultivar mesoamericano Tolima 16 que presentó un relativo alto peso de semillas requiere de una gran inversión en tejido fotosintético y los andinos México 497 y Antioquia 19 con un número relativamente bajo de hojas presentan mayor peso seco de la vainas y por ende mayor eficiencia.

Palabras clave: análisis de crecimiento, fisiología de plantas, hábito de crecimiento, evaluación.

Introduction

The bean is an annual plant that is cultivated in tropical to temperate zones. Its cultivation mainly relies on obtaining seeds that have a high protein content, around 22%. Worldwide, the cultivated area contains more than 12 million hectares and provides one of the principal sources of dietary protein for the populations of Third World countries (White and Montes, 2004). In Colombia, personal consumption is very low despite the fact that the bean is an important source of protein; according to the Ministerio de Agricultura y Desarrollo Rural, consumption is only 3.7 kg/person per year (Fenalce, 2010).

Within the group of edible legumes, the bean is one of the more important members due to its wide distribution on five continents, principally in Central and South America (Pachón, 2009). The *Phaseolus* genius includes domestic species whose wild ancestors are found in various sites from Mexico to Argentina (Singh *et al.*, 1991; Kwak and Gepts, 2009). Its domestication has generated, over a long period of time, a founder effect that lies in the establishment, by

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some individuals, of new populations that only contain a small fraction of the genetic variability of the population. The consequence of this phenomenon is low variability in the new populations of cultivated materials as compared to wild populations (Gepts, 1990). The genetic variability of the species is composed of the wild, semi-wild and domestic materials that are found in genetic diversity centers and germplasm banks.

Two bean domestication groups have been recognized; Meso-American, which contains the small seed genotypes, and Andean, which contains the large seed genotypes. Archaeological, anatomical and molecular studies produced the evidence on which these two large domestication groups are based. Koenig and Gepts (1989) recognized a third group in the northwest part of South America (Ecuador, Colombia and the north of Peru), which is the intermediate between the two large groups both at the molecular and the geographic levels.

Various studies have been carried out to characterize the genetic variability between the Meso-American and the Andean groups on the morphological and molecular levels using wild and domestic cultivars and phenotypic characteristics such as: seed size, leaf shape, leaf size, growth habits, etc.; biochemicals (phaseolins and holoenzymes) and moleculars (mitochondrial and nuclear DNA). On the other hand, studies that have measured physiological characteristics are scarce (González, 1995).

The bean produces and distributes dry material in different parts and organs in accordance with the current developmental stage. The organs compete for nutrients and water, elements that are almost always in limited supply. The organs compete for these resources and define their priorities; the reproductive tissues (flowers and pod) have first priority, followed by the leaves, roots and, finally, the stalks. Under conditions of high demand, translocation of nutrients can occur from one organ to another, for example, the mobilization of carbohydrates from stalks to pods (Chavarín *et al*., 2008).

There is evidence for the bean that demonstrates a close association between biomass production and yield. Among the yield components, the number of pods is the most affected by reductions in the production of photosynthates. Yield reductions that result from shading and yield increases that result from CO_2 fertilization support the supposition that the source is limiting. A simple method for increasing the source is increasing the growth cycle of the crop, which is directly related to the plant's growth-habit type (Chavarín *et al*., 2008).

The study of variability in the bean by evaluating physiological parameters contributes to biological and agronomic efficiency and allows for the identification of valuable germplasm that contains desirable characteristics for adaptability in determined environments. This article examines the physiological variation with growth parameters in six determinate shrub and indeterminate prostrated type bean accessions (*Phaseolus vulgaris*) under the conditions of a cold climate. The aim was to reveal the behavior of growth parameters and the accumulation of photoassimilates during the lifecycle of the crop with different Meso-American and Andean bean cultivars.

Materials and methods

Planting and harvesting was carried out in a clayey soil with moderate fertility and a pH of 5.9 at the Tibaitatá Research Center of Corporación Colombiana de Investigation Agropecuaria (Corpoica) located in the municipality of Mosquera, Colombia at 2,543 m a.s.l., with an average temperature of 12.9ºC, precipitation of 642 mm per year and relative humidity of 79%; with the coordinates 4º42' N, 74º12' W.

Six common bean collections from the Colombian germplasm bank managed by the Corpoica were used, which, according to previous studies, are representative of the grouped genetics of the Andean and Meso-American sets and contain certain morphological and physiological characteristics that are important for use as progenitors in genetic breeding for precocity, plant architecture, grain type and adaptation to the conditions of cold climates (Ligarreto, 2005; Ligarreto and Ocampo, 2012). Three accessions were taken from each genetic collection, Diacol Andino, which is commercially cultivated in the high Andean zone of Colombia, and other materials that are cultivated in small lots for self-consumption (Tab. 1).

The experimental design used random complete blocks with four replications. The parcels had four rows at a distance of 50 cm that were 4.0 m long, with 40 seeds per row planted one by one at a distance of 10 cm. Each replication sampled four plants per treatment starting at 17 d after emergence and at intervals of 8 d until the plants reached physiological maturity, for a total of 22 readings.

Evaluated variables

In total, 41 physiological variables were registered (Tab. 2). The leaf area was measured in fresh material in all the leaves of the plant using a Foliar LI-3000 (LICOR, Lincoln, NE) device; afterwards, the material was dried in a Mettler PE 3600

TABLE 1. Identification of the bean accessions from the Colombian collection.

CIAT number	Name	Growth habit	Seed size	Genetic pool
G4698	Tolima 16	3	S	M
G4700	Tolima 16 B	3	S	M
G4610	Cauca 34	3	S	M
-o- *	México 497	1	B	A
G4543	Antioquia 19	1	B	A
G5772	Diacol Andino	1	B	A

Growth habit: 1 = determinate shrub and 3 = indeterminate prostrate. Seed size: B = big and S = small, with a weight of 100 seeds of >40 and <25 g, respectively. Genetic pool: A = Andean, M = Meso-American. *Accession not present in the CIAT global collection.

(EquipNet, San Francisco, CA) oven at 70°C for 48 h to attain constant weight and determine total dry weight and the organ specific dry weights.

Measurements of net photosynthetic gas exchange and stomatal conductance were taken on a fully expanded leaf with a portable photosynthesis system (LI-6250; LICOR, Lincoln, NE) device between the hours of 9:00 and 12:00 HR using a trifoliate from the upper portion of one plant per treatment in the reproductive phase, the phenological flowering stages (R6) and the formation of veins phase (R7). The a, b and total chlorophyll contents were determined by the spectrophotometry of V4, R6 and R7 stage plant extracts at an absorbance of 649 and 665 nm.

The growth indices NAR (net assimilated rate), RGR (relative growth rate), LAR (leaf area ratio), SLA (specific leaf area), LWR (leaf weight ratio) and LAD (leaf area duration) (Tab. 2) were measured using two methods, traditional and functional. The traditional technique was proposed by Radford (1967) and its analysis was based on the use of the primary data of total dry weight, organ specific dry weight and the leaf area as measured in the field. Meanwhile, the functional technique used a lineal regression mathematical model (Hunt, 1990). The distribution of the dry material, expressed as a percentage of organ specific weight, was calculated from the total dry weight accumulated by the plant and the respective dry weights of each organ.

Statistical analysis

In the application of the formulas proposed by Radford (1967) for the fulfillment of the assumptions, it was considered: that the total dry weight of the plant continuously varies over a period of time, t_1 to t_2; and that there is a lineal relationship between total dry weight and leaf area. For the functional method, the variables of total dry weight, leaf area and dry weight of the leaves formed a natural logarithm ($\log_e$) and were adjusted to lineal models with quadratic tendencies. A Pearson association analysis was carried out for the 41 quantitative variables to eliminate some variables with high association, which were excluded in the principal components analysis. The SAS® v. 9.2 analytical program was used to process the data.

TABLE 2. Physiological variables evaluated in six bean accessions from the Colombian collection.

Variables/Unit	Variables/Unit
V1, Primary leaf area (cm^2)	V22, Net assimilation rate (NAR, g cm^{-2} d^{-1})
V2, Trifoliate leaf area (cm^2)	V23, Relative growth rate (RGR, g g^{-1} d^{-1})
V3, Total leaf area (cm^2)	V24, Leaf area ratio (LAR, cm^2 g^{-1})
V4, Root dry weight (g)	V25, Specific leaf area (SLA, cm^2 g^{-1})
V5, Stem dry weight (g)	V26, Leaf weight ratio (LWR, g g^{-1})
V6, Primary leaf dry weight (g)	V27, Leaf area duration (LAD, d)
V7, Trifoliate dry weight (g)	V28, Percentage of light interception
V8, Floral dry weight (g)	V29, Number of leaves
V9, Pod dry weight (g)	V30, Radiation (mmol m^{-2} s^{-1})
V10, Seed dry weight (g)	V31, Leaf temperature (°C)
V11, Total dry weight (g)	V32, Photosynthesis (mmol m^{-2} s^{-1})
V12, Chlorophyll a (mg m^{-2})	V33, Conductance of CO$_2$ (mol m^{-2} s^{-1})
V13, Chlorophyll b (mg m^{-2})	V34, Internal conductance to CO$_2$ (mmol m^{-2} s^{-1})
V14, Total Chlorophyll (mg m^{-2})	V35, Transpiration (mg cm^{-2} h^{-1})
V15, Proportion of dry root (%)	V36, NAR$_t$[1] (g cm^{-2} d^{-1})
V16, Proportion of dry stem (%)	V37, RGR$_t$ (g g^{-1} d^{-1})
V17, Proportion of dry primaries (%)	V38, LAR$_t$ (cm^2 g^{-1})
V18, Proportion of dry trifoliates (%)	V39, LAD$_t$ (cm^2 d^{-1})
V19, Proportion of dry flowers (%)	V40, SLA$_t$ (cm^2 g^{-1})
V20, Proportion of dry pod (%)	V41, LWR$_t$ (g g^{-1})
V21, Proportion of dry seeds (%)	

[1] Variables with $_t$ correspond to growth indices of the traditional method (Radford, 1967).

Results

Table 3 presents the summary of the variable pairs that displayed correlation coefficients above 0.90; of these variables, V1, V2, V3, V5, V14, V21, V25, V28, V34 and V35 were excluded for the principal components analysis, thereby decreasing the number of related variables that proved very difficult to measure or quantify with respect to the variable pairs (Ligarreto, 2003).

In order to differentiate the studied variables by their contribution to the physiological variation of the bean accessions, principal components statistics were used and it was determined that the first five components explained 70.33% of the variation. Tab. 4 presents the 13 variables that presented high coefficients per principal component and, by the same token, contributed the most to the variation of the bean collection. The first component explained 35% of the total variation and its associated, characteristic vector

TABLE 3. Association analysis between quantitative characteristics in the bean.

Variables	Correlation coefficient
(V2 - V3) Trifoliate leaf area - Total leaf area	0.99**
(V5 - V2) Stem dry weight - Trifoliate leaf area	0.95**
(V5 - V3) Stem dry weight - Total leaf area	0.95**
(V7 - V5) Trifoliate dry weight - Stem dry weight	0.95**
(V7 - V3) Trifoliate dry weight - Total leaf area	0.98**
(V7 - V2) Trifoliate dry weight. - Trifoliate leaf area	0.98**
(V1 - V6) Primary leaf area - Trifoliate dry weight	0.96**
(V14 - V13) Chlorophyll b - Total chlorophyll	0.96**
(V20 - V21) Percentage pod dry weight - Percentage seed dry weight	0.94**
(V25 - V22) Specific leaf area - Net assimilation rate	0.99**

** Highly significant ($P \leq 0.01$).

was represented by the variables of trifoliate dry weight (V7), dry weight of the true leaves (V18), pod dry weight (V20), LAR calculated by the functional method (V24) and by the classic method (V38) and the total number of leaves (V29), with maximum magnitude (absolute value) in their coefficients, respectively. In the component 1, the characteristics of leaf number and size could be associated with the accumulation of dry material. The components 2 to 5 presented, in the same order, decreasing percentages of variance and their characteristic vectors were represented by the variables of high coefficients as seen in Tab. 4.

Table 5 contains the average values of the 13 variables that contributed the most to the classification of the 6 accessions. Five variables corresponded to growth indices: leaf area ratio, calculated by the functional method (LAR) and the traditional method (LAR_t); and relative growth rate calculated by the traditional method (RGR_t), leaf are duration (LAD) and number of trifoliates (V29).

Seven variables corresponded to the dynamics of the dry material: dry weight of the primary leaves (V6), dry weight of the trifoliates (V7), pod dry weight (V9), seed dry weight (V10); and the variables of dry material distribution: percentage in pod dry weight (V20), percentage in dry weight of trifoliates (V18) and percentage in root dry weight (V15). The final variable corresponded to the leaf temperature (V31), a parameter related to photosynthesis. The process of photosynthesis depends on the leaf temperature because the synthesis of the enzymes that catalyze the reactions is closely linked to this factor. The branches and leaves of trees maintain a stable internal temperature that is considered ideal for photosynthesis, a process that is optimized with a leaf temperature of around 21°C, without the latitude or average temperature during the growing season playing a relevant role (Helliker and Richter, 2008).

The Meso-American cultivars were characterized by a higher dry weight of trifoliate leaves with values between 3.34 and 6.57 g/plant, while the Andean cultivars presented weights between 2.64 and 3.01 g/plant, as caused by the proportion of trifoliate dry weight that reached 36.74% in cultivar Cauca 34 with growth habit three and stems and branchings with a high quantity of leaves and small foliates that varied between 24 and 29; and the Andean cultivars presented between 10 and 14 trifoliate leaves that were large in size. On the other hand, the higher values for the

TABLE 4. Variation in the characteristic vectors, represented by the quantitative characteristics of the bean cultivars.

Variables	Component 1	Component 2	Component 3	Component 4	Component 5
V6	-0.148	0.065	0.363	0.204	-0.185
V7	0.275	0.115	0.134	-0.023	-0.010
V9	-0.116	0.420	0.157	0.074	-0.053
V10	-0.116	0.444	0.042	0.119	-0.039
V15	0.095	-0.133	-0.161	0.017	0.504
V18	0.283	0.006	-0.032	-0.011	-0.005
V20	-0.282	0.095	-0.012	-0.016	-0.079
V23	-0.063	-0.033	0.040	-0.100	0.199
V24	0.277	0.002	-0.038	0.064	-0.015
V27	0.106	-0.264	0.368	-0.133	-0.013
V29	0.289	0.018	-0.058	-0.050	0.032
V30	0.037	-0.140	0.045	-0.151	0.238
V31	-0.059	0.312	-0.351	0.127	0.010
V33	-0.043	-0.108	0.073	0.124	-0.314
V37	-0.127	0.068	-0.068	-0.454	0.127
V38	0.273	0.009	-0.108	-0.029	-0.151
V40	0.123	0.023	0.094	0.412	0.051
Proportion of variance (%)	35	13	9	8	6

TABLE 5. Quantitative physiological variables that differentiated the genetic variability of the bean cultivars.

	Meso-American cultivars			Andean cultivars		
Variables	**Tolima 16**	**Tolima 16b**	**Cauca 34**	**México 497**	**Antioquia 19**	**Diacol Andino**
V6	0.04	0.04	0.08	0.06	0.11	0.09
V7	5.88	3.34	6.57	2.64	3.01	3.01
V9	6.37	4.14	5.26	5.59	6.58	5.36
V10	3.00	1.57	1.83	2.37	2.76	2.22
V15	14.95	17.27	16.67	14.17	16.01	15.79
V18	36.74	31.61	36.28	24.87	27.90	32.63
V20	14.75	15.27	12.86	24.54	23.54	15.27
V24	125.09	96.65	110.11	79.62	92.01	104.42
V27	45.00	44	47.00	43.00	44.00	45.00
V29	27.00	24	29.00	11.00	10.00	14.00
V31	20.70	21.7	21.50	21.80	21.60	21.50
V37	0.04	0.051	0.04	0.06	0.05	0.04
V38	116.77	97.29	107.71	83.08	91.63	99.19

proportion of pod dry weight were obtained in the Andino cultivars, which varied between 15.27 and 24.54%, as compared to the Meso-American cultivars that obtained values between 12.86 and 15.27%; which is to say, the Andean cultivars had a lower number of pods but the pods were bigger and therefore contained grains of a higher weight (Tab. 5).

For LAR, the cultivars Tolima 16 and Cauca 34 presented, with the functional method, the higher average values per lifecycle, 125.09 and 110.11 cm^2 g^{-1} respectively, as compared to Tolima 16b and the three Andean cultivars. A similar behavior was seen for LAR in the traditional method with oscillations between 116.77 and 107.71 cm^2 d^{-1} for the cultivars Tolima 16 and Cauca 34; the other cultivars presented inferior behaviors (Tab. 5).

Discussion

In agreement with the assumed physiology of the growth analysis, in which a lineal ratio was established between the dry weight of the plant and the leaf area, there was a high correlation between these variables and, in addition, a high correlation was observed (r>0.95) among the variables of true leaf area (V2), total leaf area (V3) and the dry weight of the true leaves (V7), due to an increase in leaf area which is reflected in the leaf dry weight. On the other hand, the dry weight and the area of the cotyledon leaves, V1 and V6, represented a low percentage of the total foliar material due to the fact that they appear at 17 d of age of the plant and only remain for three to four weeks. The stem dry weight (V5) was highly related to the variables V2 and V3 because of the appearance of new leaves, implying the growth of the stem and the development of lateral branches (Debouck and Hidalgo, 1985).

In general, a high relationship was seen between the pods and the seeds of the bean because of the fact that these organs comprise the principal source for the required photoassimilates during the reproductive phase of plant development, in which the pods represent the organ of initial accumulation for the formation and development of the seeds; furthermore, the short distance between these organs facilitates the translocation of photosynthates from the pods towards the seeds (Martins *et al.*, 1994; Rosales *et al.*, 2004). This explains the high coefficient of correlation, 0.94 (Tab. 3), between the variables of percentage of dry weight of the pods (V20) and of the seeds (V21). In addition, if there is restriction in the number of seeds per pod, one can expect increases in their size, given the assimilation ability of the seeds as a consequence of the decrease in the number of reproductive structures (Sexton *et al.*, 1994).

Similarly, a high positive correlation was seen between the indices SLA (V25) and NAR (V22), which indicates a relationship between the productivity of the plant and the leaf thickness of the accessions. Just as the thickening of the leaves (represented by SLA) produces a decrease in CO$_2$ conductance, variations in AFE imply changes in the net photosynthesis rate in the same way that low SLA values favor the efficiency of assimilating tissues of the plant, generating an increase in NAR values (Davis and McCree, 1978; Bressan and Pereira, 2003).

The 13 variables that were selected due to their contribution in the variation of the principal components allow for the differentiation of the cultivars and, in this way, elevated RGR values with a relatively low number of leaves indicate that varieties with these characteristics are more efficient, as seen in the accessions Mexico 497 and Antioquia 19 (Tab. 5). For the latter, the relatively high primary leaf dry weight values explained the high RGR values, given that, in the initial stages of development, growth is favored because there is no self-shading effect and the accumulated weight in these leaves represents the reserve of dry material from which plant growth initiates (Eriksen and Whitney, 1984). In the component 2, it is interesting to note that the variables with greater contribution in a positive sense are V9, V10, and V31; and in a negative sense, V27, demonstrating that there is a balance between the dry weight of the pods and seeds and the leaf temperature, in contrast to the duration of the leaves. So, the genotypes that had the higher leaf temperatures could transport their assimilates in a more efficient manner to the grains and pods under these conditions but they lasted for a shorter time, a situation that could be different in other locations or under heat-stress conditions.

In the description of the cultivar groups, one could say that the three Meso-American cultivars are as efficient as the Andean cultivars because they present a superior number of leaves and, even with a high LAR, seen as the ratio of assimilation material per unit of plant material (Ligarreto, 2013), the highest RGR values are not seen on average; specifically, Tolima 16, which presented a relatively high seed weight, required a large investment in photosynthetic tissue.

The cultivar Tolima 16b presented a low value for primary leaf dry weight but the average RGR was high. This could indicate that during this stage of development (V2 = primary leaves), this variety is very efficient, presenting a good growth rate with minimal investment in photosynthetic tissue. However, it did not present a good behavior for yield due to the fact that the dry weight accumulated in the seeds was relatively low (1.57 g), possibly because of the poor adaption of this accession in cold climates, which could indicate deficiencies in the process of dry material translocation during the final phases of the plant's lifecycle (Bayuelo *et al*., 2002).

The Cauca 34 material was the least efficient because it presented a high number of trifoliates and, therefore, a high weight for the true leaves, but low values for RGR; in addition, the percentage of accumulated weight in the pods was the lowest (12.86 g), indicating that this material, despite presenting a high proportion of photosynthetic tissue, did not have a good behavior in the translocation of assimilates. It appears as though this accession designates a large part of the produced material to the formation of leaves but it is not very efficient in the translocation of theses photosynthates in the final cycle during the formation and filling of the pods, which constitute the primary material for the formation of the seeds (Díaz, 1990).

Conclusions

Mexico 497 and Antioquia 19 of the Andean pool, with large seeds, presented a good physiological behavior in the conditions of the cold climate because they attained a high accumulation of dry material in the seeds with a low investment in the production of photosynthetic tissue and good translocation of photoassimilates in the pods and seeds.

There was a high association between the genetic pools and the size characteristics of the leaves and large seeds in individuals of the Andean group; and small seeds in the Meso-American group.

The evaluated accessions are assets that are available to the producers and were chosen due to the characteristics of the crop and due to commercial acceptance in the local markets of Colombia. Currently, these varieties could be recovered by the farmers and their use could again be promoted in local areas. Furthermore, these results can be used in future studies on the selection of progenitors for genetic improvement programs.

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