Differences in growth and water relations among Phaseolus vulgaris cultivars in response to induced drought stress

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Abstract

Relatively little ecophysiological research has been conducted to determine the responses to drought of Phaseolus vulgaris. Four bean cultivars ( cvs.) from Brazil, A320, Carioca, Ouro Negro and Xodó were submitted to an imposed water deficit in order to evaluate the importance of some adaptive mechanisms of drought resistance through the analysis of growth parameters, water status, gas exchange and indicators of tolerance mechanisms at the cellular level. During the drought treatment, relative growth rates were more reduced for A320 and Xodó than Carioca and Ouro Negro. A320 closed its stomata very rapidly and complete stomatal closure was obtained at \( \Psi_w = -0.6 \) MPa, in contrast to the other cvs. where stomata were fully closed only at \( \Psi_w = -0.9 \) MPa. Net assimilation rates were closely related to stomatal conductances. Mechanisms at the cellular level appeared to be mostly important for higher tolerance. Carioca and Ouro Negro, when compared to A320 and Xodó, were characterized by having better drought tolerance mechanisms and higher tissue water retention capacity leading to a better growth under water deficits. The leaf dehydration rates of those cvs. were slow whereas those of the drought sensitive cvs. were rapid. The results were confirmed by the electrolyte leakage test and leaf osmotic potential measurements, which indicated higher membrane resistance and osmotic adjustment in the two tolerant cvs. Carioca and Ouro Negro. It appears from this study that despite being cultivated in the same geographical region, the four cvs. of P. vulgaris displayed somewhat different drought adaptive capacities for prolonged drought during the vegetative phase. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Drought; Growth; Membrane damage; Net assimilation rate; Osmotic potential; Phaseolus vulgaris; Stomatal conductance

Abbreviations: A, assimilation rate; Gs, stomatal conductance; H, humidity of substrate; PEG, polyethylene glycol; RWC, relative water content; \( \Psi_w \), leaf pre-dawn water potential.
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1. Introduction

Bean grains are important protein sources for many developing countries (Markhart, 1985). There exists in the world ten important gene pools of Phaseolus species (Singh, 1989); six of them belong to the Central American and four to the South American domestication centers. Phaseolus vulgaris is the most cultivated bean species in these areas and contribute to 90% of the total bean production (Graham and Ranalli, 1997). As much as 60% of bean production in the developing word occurs under conditions of significant drought stress (Graham and Ranalli, 1997). It is therefore important to elucidate the drought tolerance mechanisms of this species in order to improve its agronomic performances and to obtain more resistant cultivars (Subbarao et al., 1995).

As much field and greenhouse observations as experimentation in controlled environments have shown that P. vulgaris is relatively sensitive to drought stress compared to other grain legumes (Haterlein, 1983; Pimentel et al., 1990; Salinas et al., 1996; Cruz de Carvalho et al., 1998; Pimentel, 1998). In cultivars of P. vulgaris studied so far, one of the first effects observed after dehydration is stomatal closure, even before detection of any leaf water deficit (Trejo and Davies, 1991; Barradas et al., 1994; Cruz de Carvalho et al., 1998). However, genetic variability within P. vulgaris germplasm for drought stress has not been assessed. Field research has been showing differences in growth and grain yield among cultivars when submitted to drought conditions during the growing season (Bergamaschi et al., 1988). Therefore, it can be supposed that differences exist among them, that could be linked to differences in adaptive drought mechanisms.

The two main components of drought resistance in plants are drought avoidance and drought tolerance (Levitt, 1980; Turner, 1991). In common beans, the mechanisms of drought avoidance include principally the development of an extensive root system and an efficient stomatal closure (Haterlein, 1983; Trejo and Davies, 1991; Barradas et al., 1994). Mechanisms of drought tolerance, especially at low plant water status, involve processes at the cellular level, the most important being osmotic adjustment and protection of the membrane system (Pham Thi and Vieira da Silva, 1975; Turner and Jones, 1980; Mullet and Whitsitt, 1996). The osmotic adjustment can allow the maintenance of root or shoot growth under stress conditions, through a control on cellular turgor (Creelman et al., 1990; Mullet and Whitsitt, 1996). Structural integrity of cellular membranes is also important for survival under severe dry periods, or in situations where random droughts occur (Turner and Burch, 1983). Seedling survival and survival during the vegetative phase are important in obtaining yields under drought (O'Toole and Chang, 1979).

Working hypotheses were that differences exist in drought resistance among P. vulgaris cultivars and that such differences are expressed in the vegetative phase of growth. To test that hypothesis we accomplish an experiment where four bean cultivars were submitted to a period of progressive water deficit by suppression of irrigation. During this induced drought period leaf area production and relative growth and gas exchange rates were evaluated in relation to leaf water status. Also, a test of electrolyte leakage in response to an osmotic shock was included as a probe for a possible drought adaptation at cellular level. Such a leakage has been used as a measure of the extent of membrane damage resulting from the desiccation/rehydration event (Oliver, 1996).

2. Materials and methods

2.1. Plant materials and culture

Four cultivars of P. vulgaris L., A320, Carioca, Ouro Negro and Xodo, all in cultivation in Brazil, were selected on the basis of greenhouse and fields observations, that showed differences in growth and yield under irrigated or non-irrigated conditions (Pimentel et al., 1990; Gomes et al., 1999). Seeds were pre-germinated for later selection for seedling uniformity. One-liter pots were filled with 800 g of mix fertilized peat (TKS® instant, Floragard, UK) and vermiculite (1:1) and irrigated to maximum water retention capacity of the
substrate. *Rhizobium* bacteria were added neither to the soil nor to the seeds, in order to eliminate eventual artifacts due to the effects of drought on the root nodules. According to the manufacturer, nutrient elements furnished to the peat could ensure plant growth for approximately 2 months. The plants were irrigated daily with distilled water to maximum retention capacity and the pots sealed with plastic film in order to avoid evaporation loss. The environmental conditions of the phytotron were adjusted to 12-h photoperiod, with temperature ranging between 28 and 24°C, and relative humidity between 50 and 80% between day and night. The photosynthetic photon flux density (PPFD) was greater than or equal to 600 \( \text{mmol m}^{-2} \text{s}^{-1} \). Experiments were performed between the 15th and 25th day after sowing (DAS).

### 2.2. Experimental design and water regimes

Pots were placed randomly and at 15 DAS the irrigation was suspended in half of them for each variety. The humidity of the substrate \((H)\) was calculated as the % of the actual water weight compared with the weight at maximum water retention of the substrate. The drought treatment lasted 10 days, the pot weights were determined daily. The experiment was treated as a 4 cultivars \(\times\) 2 water treatments (drought and control) factorial with an average of four individuals. Primary data were previously submitted to normality parametric and homocedastly test posterior to variance analysis. Data were analyzed using the statistical analysis system (SYSTAT, 1990–1992). Means were separated with Tukey multiple range test at \(P \leq 0.05\). Regression was used to determine the relationship between the different parameters.

### 2.3. Growth measurement

Leaf and stem dry weights and plant total dry weight (TDW) were determined at 15 and 25 DAS for control and drought-stressed plants of each cultivar. Leaf area was also measured for each collecting period plants (Area meter-RS 232 C, AT Devices, Cambridge, UK). From these values, relative growth rates (RGR) and specific leaf area (SLA) were calculated from the following expressions (Hunt, 1978):

\[
\text{RGR} = \frac{\ln W_2 - \ln W_1}{T_2 - T_1} \\
\text{SLA} = \frac{\left( \frac{\text{LA}_1}{\text{WL}_1} \right) + \left( \frac{\text{LA}_2}{\text{WL}_2} \right)}{2}
\]

where, \(W\), plant dry weight; \(WL\), leaf dry weight; \(LA\), leaf area; \(T\), time; and subscripts 1 and 2 correspond to successive collections. This procedure was adopted in order to reduce differences.

### 2.4. Leaf gas exchange measurement

Stomatal conductances to water vapor (Gs, \(\text{mmol m}^{-2} \text{s}^{-1}\)) and net photosynthetic rates \((A, \mu\text{mol m}^{-2} \text{s}^{-1}\)) were determined on the uppermost fully expanded leaves, using a Parkinson leaf chamber connected to two differential infrared gas analyzers for CO\(_2\) and H\(_2\)O vapor (ADC 225-MK3, Hoddesden, UK), and a computer for data processing. Measurements were carried out under light-saturating conditions (i.e. at PPFD higher than 600 \(\mu\text{mol m}^{-2} \text{s}^{-1}\)). The air was pumped into the system at a flow rate of 0.4 l min\(^{-1}\), with CO\(_2\) input of 375 \(\mu\text{mol mol}^{-1}\). Atmospheric water vapor pressure deficit (VPD) inside the assimilation chamber was kept below 500 Pa. The other microclimatic conditions prevailing in the assimilation chamber matched those of the outside atmosphere. Leaf temperature was calculated from leaf energy balance equation (Parkinson, 1984). Gs and A were calculated according to Von Caemmerer and Farquhar (1981). VPD was calculated as the difference between partial water vapor pressure of leaf internal air, taken to be equal to saturating vapor pressure (at leaf temperature) and partial water vapor pressure of the exiting air (at chamber air temperature).

### 2.5. Leaf water status

Measurements of leaf water status were carried out at predawn. \(\Psi_w\) was determined with a pressure chamber (Scholander et al., 1965; PMS Corvallis, USA) in the apical part of the trifoliate tightly enclosed in a plastic bag before excision. RWC was measured with six leaf discs per plant. Full saturation was determined on leaflets rehy-
drated for 20 h at 5°C in the dark. Control and stressed trifoliates without veins were rapidly cut and enclosed in a plastic bag, in order to perform cellular rupture at −20°C. The osmotic potential ($\Psi_0$, MPa) was measured in the juice obtained by pression on the plastic bag with an osmometer (Roebling automatik, Illkirch, France).

2.6. Electrolyte leakage measurements

Leaf discs (0.8 cm diameter) were punched from fully expanded leaves of 25 DAS control plants. Eighty leaf discs were rinsed three times for 30 min with distilled water to remove solutes from damaged cells and veins. Forty discs per replicate were then floated for 4 h under light and at room temperature, either on distilled water (control) or on PEG (polyethylene glycol) solution (MW 6000, −1.4 MPa osmotic potential). After PEG treatment, the discs were rapidly rinsed three times and floated on distilled water for 24 h in the dark at room temperature. The conductivity of the solutions was measured with a conductometer (Tacussel CM-02-SJ-6, Lyon, France). The Injury Index (I%) was expressed using ion leakage according to Vasquez-Tello et al. (1990).

3. Results

3.1. Relation between substrate water content and leaf water potential

Fig. 1 shows a non-linear regression with two decaying exponential phases obtained from the relationship between available substrate water content ($H$) and leaf predawn water potential. The resulting mathematical relation between $H$ and water potential was:

$$\Psi_w = -1.27 + 0.73 (1 + \exp(39.15 - H/11.5))$$

$R^2 = 0.81, P < 0.0001$. With $H$ up to 65%, water potential of leaves remained high and unchanged. Below this value, soil water availability became limited and leaf water potentials decreased abruptly, attaining maximum values of −1.2 MPa with $H = 8\%$ and after 10 days of drought treatment. This equation was then be used to estimate leaf water potentials from $H$ measurements made during the drought treatment on the four cultivars of $P$. vulgaris, since for all cultivars, the curves ($\Psi_w$ vs. $H$) were not significantly different, having similar average values.

3.2. Effect on plant growth

Drought stress reduced plant growth in all four cultivars (Table 1). In control conditions, Xodo is the most fast-growing cultivar. Well-irrigated plants of this cultivar produced more TDW, and had higher leaf area than the other cvs. Under stress, the TDW of Xodo decreased by 47% but the TDW of droughted plants was not significantly different from the other cvs. SLA, as an indirect measure of leaf thickness was not significantly affected during stress.

The relative growth rates (Table 2) confirmed the results of Table 1. Xodo and Carioca had the best growth performances and A320 the lowest RGR. It appears also from Tables 1 and 2 that Carioca is an interesting cv., presenting a good growth potential when normally irrigated, and having a relatively good resistance to water stress. A320 on the contrary seems to be the less interesting of all. In fact, its growth performances were low (Total RGR = 0.14) and it resisted badly to drought (Total RGR = 0.09). RGR of Ouro
Table 1

TDW, LA and SLA in four cultivars of *P. vulgaris*, with or without exposure to water deficit for 10 days*.

<table>
<thead>
<tr>
<th></th>
<th>TDW (g)</th>
<th>LA (m²)</th>
<th>SLA (m² g⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Control</td>
<td>Drought</td>
<td>Control</td>
</tr>
<tr>
<td>A320</td>
<td>4.47 a</td>
<td>2.68 c</td>
<td>0.132 a</td>
</tr>
<tr>
<td>Carioca</td>
<td>4.22 a</td>
<td>2.71 c</td>
<td>0.137 a</td>
</tr>
<tr>
<td>O. Negro</td>
<td>3.74 a</td>
<td>2.66 c</td>
<td>0.144 ab</td>
</tr>
<tr>
<td>Xodó</td>
<td>5.48 b</td>
<td>2.91 c</td>
<td>0.155 b</td>
</tr>
</tbody>
</table>

*Values sharing a common letter in each column (parameter) or each line (cultivars) are not significantly different at *P* ≤ 0.05 level of Tukey’s test. The experiment had four replications.

Table 2

Mean RGR of leaf, stem and whole plant in four cultivars of *P. vulgaris*, with or without exposure to water stress for 10 days*.

<table>
<thead>
<tr>
<th></th>
<th>Leaf RGR (g g⁻¹ d⁻¹)</th>
<th>Stem RGR</th>
<th>Total RGR (g g⁻¹ d⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Control</td>
<td>Drought</td>
<td>Control</td>
</tr>
<tr>
<td>A320</td>
<td>0.11 a</td>
<td>0.07 a</td>
<td>0.20 a</td>
</tr>
<tr>
<td>Carioca</td>
<td>0.17 b</td>
<td>0.14 b</td>
<td>0.26 b</td>
</tr>
<tr>
<td>O. Negro</td>
<td>0.11 a</td>
<td>0.09 ac</td>
<td>0.18 a</td>
</tr>
<tr>
<td>Xodó</td>
<td>0.19 bd</td>
<td>0.13 bc</td>
<td>0.24 ab</td>
</tr>
</tbody>
</table>

*Values sharing a common letter in each column (parameter) or each line (cultivar) are not significantly different at *P* ≤ 0.05 level of Tukey’s test. The experiment had four replications.

Negro under control and stress conditions were low (Table 2), but the reduction in TDW of this cv. (Table 1) was less than that of the others.

3.3. Response of stomatal conductance to substrate water supply

The response of Gs to decreasing *H*, *Ψ*ₙ and RWC is shown in Fig. 2(A, B and C), respectively. The data were expressed as percentages of mean maximum values obtained for well-hydrated plants. As substrate water content decreased below 30%, stomatal conductance decreased linearly to its minimum value (Fig. 2(A)). Under high hydration conditions, no great differences were observed between cultivars, although A320 showed a slightly higher stomatal opening. On the onset of drought stress, however, the behavior of the four cvs. diverged: A320 showed a more rapid Gs decrease with stomatal closure beginning at *H* = 30% hydration, earlier than the other cvs. Xodó kept stomata open at hydration values around *H* = 12%.

Fig. 2(B) shows response of Gs to *Ψ*ₙ variation. Almost complete stomatal closure occurred at *Ψ*ₙ values of −0.9 MPa, but A320 had an abrupt response after *Ψ*ₙ = −0.52 MPa, and a sigmoidal behavior was observed for the remaining cvs. Xodó closed its stomata later than the other cvs.

Responses of Gs to decreasing leaf RWC are shown in Fig. 2(C). Stomatal conductance was more sensitive to RWC than other evaluated parameters, with sharp decreases between 93–94% and 92% linear responses until RWC 91%. A320 showed complete stomatal closure at 92% RWC, and the other cvs. kept Gₛ at about 10–20% of their maximum, even in conditions of severe drought.
3.4. Response of net assimilation rate to substrate water supply

The response of $A$ to decreasing $H$, $\Psi_w$ and RWC is shown in Fig. 3(A, B and C), respectively. With adequate availability of soil water, until $H = 30\%$, we did not observe any difference in the net assimilation rate between cultivars (Fig. 3(A)). Zero values of $A$ were obtained at $H = 7\%$. The decline in $A$ for A320 began as soon as $H$ reached 30\%. At $H = 15\%$, A320 showed net assimilation rates at about 20\% of the control, while Xodô kept $A$ levels close to those of well hydrated plants. Therefore, Xodô may be capable of maintaining high net assimilation rates when submitted to moderate drought stress.

Net assimilation rates dropped to near zero at $\Psi_w = -1.0$ MPa for Xodô, Carioca and O. Negro and at $\Psi_w = -0.6$ MPa for A320. At $\Psi_w = -0.6$ MPa, Xodô, Carioca and O. Negro maintained $A$ between 50 and 90\%. Values of $A$ for plants submitted to water stress were more correlated to $\Psi_w$ and RWC than to the available water in the soil. At RWC of 93\%, assimilation rates decreased, reaching minimal values at RWC of 90\%. The RWC interval that allowed stomatal closure and minimal assimilation rates was very small (Fig. 2(C) and Fig. 3(C)).

3.5. The relationship between assimilation rate and stomatal conductance

Fig. 4 presents the relation between $A$ and $G_s$. Except for A320, we can observe two distinct phases in the curves. Phase I corresponded to high $G_s$ and a large variability in $A$, which was not limited by stomatal conductance. Phase II started when $G_s$ was substantially reduced (below approximately 0.1 mol CO$_2$ m$^{-2}$ s$^{-1}$). During this phase, $A$ was linearly correlated with stomatal aperture. The parameter ($A \times G_s$), also called intrinsic efficiency of water use (IEWU), allowed the discrimination of plants that maintained CO$_2$ assimilation at low stomatal aperture. This was the case for Carioca and Xodô, which presented higher IEWU values; A320 on the other hand, had the lowest values. The behavior of A320 was also very different from the three others cvs., since

![Fig. 2. Effect of drought stress expressed as substrate water content ($H$) (A), as predawn water potential ($\Psi_w$) (B), as leaf RWC (C), on leaf stomatal conductance (% mol H$_2$O m$^{-2}$ s$^{-1}$ maximum). A320 (□---), Carioca (△--○), Ouro Negro (○--·), Xodô (◇-----).](image-url)
A was closely dependent on $G_s$, over the whole treatment. Moreover, $G_s$ was very high when the plant was well irrigated, which indicates, either a large opening of the stomata, or a high stomatal density.

3.6. Dehydration rate-water retention capacity and protoplasm tolerance

Control plants showed little genetic variability at predawn RWC and $\Psi_w$ (Fig. 5). At the time of stomatal closure (Fig. 2(B), $\Psi_w = -0.75$, Fig. 2(C), RWC = 92%), RWC and $\Psi_w$ declined, but there was no difference among the cultivars. $\Psi_w$ and RWC continued to decline after stomatal closure, indicating that the plants continued to lose water (Fig. 5). However, the rate of decline in RWC and $\Psi_w$ from stomatal closure until the end of the dehydration period varied significantly ($P \leq 0.0001$) among cultivars. At the end of treatment, it was thus possible to separate the cultivars according to their dehydration rate: fast for A320, slow for Carioca and O. Negro and intermediate for Xodó. These differences were found in all four replications.

Fig. 3. Effect of drought stress expressed as substrate water content ($H$) (A), as predawn water potential ($\Psi_w$) (B), as leaf RWC (C), on photosynthetic assimilation rate ($\% \mu$mol CO$_2$ m$^{-2}$ s$^{-1}$ maximum). A320 (□—□), Carioca (△—△), Ouro Negro (○—○), Xodó (◇—◇).

Fig. 4. Net assimilation rate (A) versus stomatal conductance ($G_s$), measured on drought-stressed leaves of P. vulgaris cultivars. A320 (□—□), Carioca (△—△), Ouro Negro (○—○), Xodó (◇—◇).
4. Discussion

In this study, four cultivars of *P. vulgaris* were compared regarding their resistance to an imposed water stress in controlled conditions during the early vegetative stage. Results showed that although being cultivated in the same geographic area, the four cvs. display distinct responses to a prolonged drought stress. Growth analysis indicate that the cvs Xodó and Carioca, which presented the best growth in conditions of good hydration of the soil, were potential material of larger agronomic interest. However, Carioca becomes a more interesting material than Xodó in conditions of drought stress, due to its ability to maintain relatively high relative growth rates.

Net assimilation rates were differently affected among the four cultivars, i.e. fast reduction in A320, intermediary in Carioca and Ouro Negro and slow in Xodó (Fig. 3). The decline of CO$_2$ uptake is supposed to be dependent on stomatal closure and on non-stomatal components. It is now well established that in condition of moderate water deficit, the photosynthetic apparatus is not damaged. It continued to function, thanks to coupling with photorespiration (Brestic et al., 1995), as attested by photochemical measurements (Sharkey and Badger, 1982) and estimations of internal CO$_2$ concentrations (Ci; Donovan and Ehleringer, 1994). On the other hand, when the plant was submitted to severe water deficit, and its water potentials fell below of a certain threshold (variable according to the species), the photosynthetic capacity decreased, as attested by the increase of Ci (Brodribb, 1996) and decrease in Rubisco activity (Vu et al., 1998). Our results evidenced the close relationship between stomatal conductance and the reduction of the assimilation
rates (Fig. 4). In *P. vulgaris*, it was difficult to have correct measures of $C_i$, due to stomatal patchiness, but it is probable that in conditions of prolonged drought as those of this study, $A$ and growth impairment were not only due to stomatal closure, since our previous studies had shown a slower and partial recovery following rehydration after drought (Cruz de Carvalho et al., 1998).

In conditions of good water supply, stomata were more open in A320 than in the other cvs. (Fig. 2), however, this cv also closed its stomata more rapidly. Stomatal closure may be a common drought avoidance response allowing plants to keep water in their tissues (Ludlow, 1980). However, it also restricted the entry of $CO_2$ to mesophyll cells, and consequently reduced net photosynthetic rates. Effectively, A320 which closed its stomata rapidly, also presented the highest reduction in RGR (Table 2). Carioca and Ouro Negro, which closed their stomata more slowly, maintained $CO_2$ assimilation longer and had less reductions in RGR. Despite stomatal closure, A320 lost its leaf water more severely than the other cvs. (Fig. 5), probably because higher cuticle transpiration and the incapacity to retain water by lowering leaf osmotic potential. Effectively, in the cvs that keep their leaf water better (Carioca and Ouro Negro), lowering of osmotic potential was more important (Table 3). This was not a concentration effect because leaf RWC remained high, but may be a result of osmoregulation. Osmotica like free amino acids, sugars, often accumulate in plants submitted to water deficits (Steward and Hanson, 1980; Schwab and Gaff, 1986; Premachandra et al., 1992). Besides their effect on the cell water retaining capacity, they also protect membranes and macromolecules by maintaining around them a water shell (Schobert and Tschesche, 1978; Crowe et al., 1988). Plants that possess drought tolerance at the cellular level were often able to maintain stomata open at severe water deficits. This allows a net $CO_2$ uptake, even during a severe drought since it is well established that photosynthetic mechanisms are resistant to water shortage (Brestic et al., 1995). This is the case for Carioca and Ouro Negro (Fig. 3(C)). These cultivars are also those that present the lowest membrane injury index when submitted to the electrolyte leakage test (Fig. 6). Despite the fact that dehydration stress under field conditions is very different from PEG-induced stress in leaf discs, this test allowed us to have an idea on the resistance of the cell membrane system (Murray et al., 1989). Various authors have suggested the use of the leakage test as a measure of protoplasmic tolerance in legumes (Krishnamani et al., 1984; Premachandra et al., 1990; Vasquez-Tello et al., 1990).

In conclusion, the results of our research pointed out the need for using integrated traits when evaluating drought resistance of plants. Early stomatal closure, photosynthesis and growth, water retention of tissues, osmotic potential and membrane resistance are useful parameters, but relationship between each of them and drought resistance of the plant could be complex and depend on the intensity and the duration of drought. In case of short periods of water deficits, stomatal closure is an efficient adaptive response, but during prolonged drought, specific biochemical mechanisms at the cellular level allowed plants to resist better. This is illustrated by the results of this study. Further studies are necessary to clarify the adaptive responses in *P. vulgaris* cvs., in particular during the vegetative stage, the behavior of the root system, the nature of the accumulated osmolytes, and the capacity to return to normal physiology during post-stress rehydration.

Little information is available regarding genotypic variation for drought tolerance in legumes (Subbarao et al., 1995). This study should help understand some adaptive mechanisms developed by *P. vulgaris* and contribute to identify useful traits for breeding programs.

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