

Correlation between yield and osmotic adjustment of peas (*Pisum sativum* L.) under drought stress

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ABSTRACT

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This work examines the relationship between the osmoregulation capability of various pea cultivars and breeding lines, grown in climatic chambers (subjected to one dehydration cycle), and their yields in the field under drought conditions. The relative water content at an osmotic potential of -1.5 MPa was used as an indicator of osmoregulation. There was a linear relationship between yield and osmotic adjustment in two years ($R=0.70$ and $R=0.92$), but not in a rainy year, when drought stress was slight.

INTRODUCTION

Osmoregulation has been shown to be an effective drought tolerance mechanism in a number of crop species (Ackerson et al., 1980; Morgan, 1980, 1984; Turner et al., 1986; Oosterhuis and Wullschleger, 1987).

Some authors have demonstrated that there is genetic variation for osmoregulation within a species (Morgan, 1977, 1984). It has also been established that drought resistance, defined as greater yield under water stress, is associated with osmoregulation, in both durum and bread wheats (Morgan, 1983; Morgan and Condon, 1986; Morgan et al., 1986). Blum et al. (1983) found an association between osmoregulation and the growth of wheat in solution culture. In wheat, this trait is probably controlled by a single gene (Morgan, 1983). The association between the osmoregulation capacity and yield under water stress conditions, and the probable simple inheritance of this character, makes it a promising trait for introduction into breeding lines.

In this work, we have studied the osmoregulation capacity of various pea

cultivars and breeding lines (both referred to hereafter as lines), subjected to progressive water stress in climatic chambers, and its association with their grain yield when grown in the field under drought conditions.

MATERIALS AND METHODS

Seven pea lines forming part of a commercial plant breeding program were evaluated in the field and in growth chambers (Table 1). Some lines were semi-leafless, having their leaflets transformed to tendrils.

Field experiments

Three field experiments were carried out on the experimental farm 'La Canaleja' (Madrid), on a sandy clay loam soil (calcic haploxeralf). Sowings were 14 January 1986; 22–23 January 1987; and 14 February 1988. The lines were sown in rows, perpendicular to line source sprinklers, so that individual plants received decreasing amounts of water the further they were from the line of sprinklers (Hanks et al., 1976).

Each line was sown in six rows 0.30 m apart, with population densities of 475 000, 696 000 and 613 000 plants ha⁻¹ in 1986, 1987 and 1988, respectively. To estimate yield, grain was collected from 1.2 m² areas, at various distances from the line sprinklers. Four replications were measured in 1987 and 1988, and two in 1986.

Irrigation was sufficient to replace potential evapotranspiration by the plants adjacent to the line. Four sets of catch cans (two in 1986), distributed 2 m apart in rows perpendicular to the line of sprinklers, were used to estimate the amounts of irrigation received at progressive distances from the line.

Evapotranspiration was estimated by the water balance technique assuming that the variation of water in the soil, measured with a neutron probe

TABLE 1

Pea lines evaluated in the studies

Pea lines reference	Name, origin and characteristics
V-2	F4 (1986), F5 mass (1987) and F6 mass (1988), from Frisson × Filby, semi-leafless
V-4	Frisson, commercial cultivar, conventional leaves
V-6	Desso, commercial cultivar, conventional leaves
V-8	Amino, commercial cultivar, conventional leaves
V-9	Fride, commercial cultivar, conventional leaves
V-12	F5 (1986), F6 mass (1987) and F7 mass (1988), from Desso × Filby, semi-leafless
V-13	F5 (1986), F6 mass (1987) and F7 mass (1988), from Lysima × Frisson, conventional leaves

(Nardeux, mod. Solo-20, Z.A. de Courtaboeuf, Les Ulis, France), results from addition by rain and irrigation and loss by evapotranspiration.

In 1987 and 1988, fertilizer application was 30 kg N ha⁻¹, 35 kg P ha⁻¹, and 116 kg K ha⁻¹. In 1986, it was 30 kg N ha⁻¹, 13 kg P ha⁻¹ and 25 kg K ha⁻¹. Plots were treated with herbicides and hand weeded.

The experimental design was the strip split plot described by Cochran and Cox (1957).

Laboratory experiments

Plants were grown in climatic chambers in pots of 10.5 cm diameter, having vermiculite as substrate. After germination, a complete nutrient solution was used on three out of four irrigations.

Photosynthetically active photon flux density, measured at the tops of the plants, was 317 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Photoperiod was 16 h, and day/night temperatures were 21/16°C.

Water was withheld from the plants when they were 25 days old. Leaf osmotic potential (OP) and relative water content (RWC) measurements were made on the uppermost fully expanded leaf. Osmotic potential was measured on leaflets, and RWC measured upon three or four discs from the complementary leaflet of each leaf. Leaf osmotic potential of detached leaflets was measured with a dew point hygrometer (Wescor microvoltmeter, mod HR-33T and C-52 sample chamber, Wescor Inc., Logan, UT, USA) at 11–13 days after withholding water, after freezing by immersion in liquid nitrogen and thawing at ambient temperature. Frozen leaves were placed in a 1.0 cm³ hypodermic syringe and sap expressed onto a filter-paper disc, which was then placed in the sample chamber. Equilibration time was 5 min. Leaf relative water content was measured by floating leaf discs on distilled water for approximately 16 h at 1°C, in the dark (Milburn and Weatherley, 1971). Leaves were always sampled 2 h after the daily light period started. There were three replications for each measurement of OP and RWC.

When measurements were taken on semi-leafless lines, the stipules were used instead of leaflets. It was verified that OP and RWC did not differ significantly between stipules and leaflets from the same leaf of conventional-leaf lines.

RESULTS AND DISCUSSION

Table 2 presents the mean grain yields and the amounts of irrigation water in relation to the distance of the sampled plots from the line source sprinklers. For each year in which the field experiment was performed, it was possible to establish a linear correlation between mean grain yield and the amount of water (Fig. 1).

TABLE 2

Pea grain yields (g m^{-2}) and amounts of irrigation water in relation to the distance to the line source sprinklers (1986, 1987 and 1988). Total rainfall during the growth period also shown. In each year, values with the same letter are not significantly different at $P=0.01$ (capitals) or $P=0.05$ (lower-case) by Duncan's multiple range test

Distance to Sprinklers (m)	Pea lines							\bar{X}	Irrig. water (mm)	Rainfall (March-mid June, mm)
	V-2	V-4	V-6	V-8	V-9	V-12	V-13			
1986										
4	278	264	301	266	243	342	355	292.7a	188.9	85.4
6	242	321	189	269	197	334	266	259.7a	166.4	
8	185	201	189	184	223	272	222	210.9b	120.2	
10	190	168	160	175	174	224	186	182.4bc	67.4	
12	169	140	155	143	116	174	156	150.4cd	25.1	
14	128	115	148	124	122	173	118	132.6d	5.3	
\bar{X}	199AB	202AB	190AB	194AB	179AB	253A	217AB			
1987										
4	424	405	561	389	356	474	463	438.9a	214.2	97.5
6	405	335	515	411	391	462	479	428.3a	195.0	
8	336	326	475	358	325	387	398	372.1	120.6	
10	263	223	319	263	224	286	267	263.6	44.4	
12	196	188	250	226	217	243	193	216.1b	12.0	
14	206	183	217	198	234	227	218	211.9b	2.7	
\bar{X}	305BC	277C	390A	308BC	291BC	347AB	336ABC			
1988										
4	380	368	467	504	259	527	427	418.8a	52.5	191.5
8	357	338	343	518	273	450	414	384.7a	32.3	
12	317	366	227	388	232	287	246	294.8b	12.3	
16	190	278	278	287	230	230	205	242.4b	1.8	
\bar{X}	311BC	338ABC	329BC	424A	249C	374AB	323BC			

The relationships between the natural logarithms of relative water content and the natural logarithms of osmotic potentials, for each line measured in one dehydration cycle, are shown in Fig. 2. There is a two step response for each line, except for V-6. The abscissa of each vertical straight line is the mean of the natural logarithm of the relative water content of its constituent points; while the inclined lines have been drawn to obtain the best fit to their points. For the purposes of comparison of these responses, the relative water content at a given osmotic potential was used (Morgan, 1983). An OP of -1.5 MPa (rather than -2.5 MPa for wheat) was chosen as it was at the limit of measured osmotic potential for several pea lines, and it allowed a reasonably good discrimination among them (Morgan, pers. commun., 1988).

Fig. 3 shows statistically significant, positive relationships between yield in stress conditions (mean yield at 12–14 m from the line in 1986 and 1987) and osmotic adjustment expressed as relative water content for an osmotic potential of -1.5 MPa.

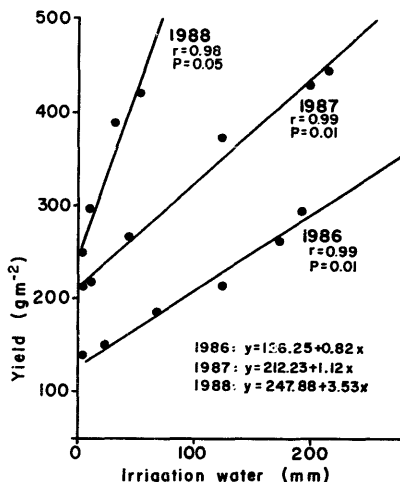


Fig. 1. Correlations between mean grain yields (of all the pea lines), and amounts of water provided.

Precipitation data (Table 2), and direct observation indicated that the plants rarely suffered water stress during 1988. The rain registered in that year during the period of active growth (March till mid June), was more than double that registered for the same period in 1987 or 1986. Accordingly, it was necessary to irrigate only twice in 1988, adding a total of 52.5 mm (Table 2) adjacent to the line source sprinklers. The existence of water stress, at least in the plants that did not receive the maximum irrigation during 1986 and 1987, is demonstrated by the strong linear correlations between yield and the amounts of water applied (Fig. 1).

When plants are subjected to water stress, their osmotic potential tends to decrease. If this decrease does not accompany a change in relative water content, there is full osmoregulation. If however, the relative water content decreases, this will indicate a higher or lower osmoregulation depending on the magnitude of the decrease (Morgan, 1977).

Results in Fig. 2 indicate that in our case the relations between the natural logarithms of relative water content and osmotic potential show generally a similar pattern for all the lines. In the first stages of the stressing process, relative water content did not decline, shown by the vertical line. As water stress intensified, the line fell steeply, in keeping with the osmoregulation of each line. We have used an estimated value of relative water content for an osmotic potential of -1.5 MPa, as an indicator of the capacity for osmotic

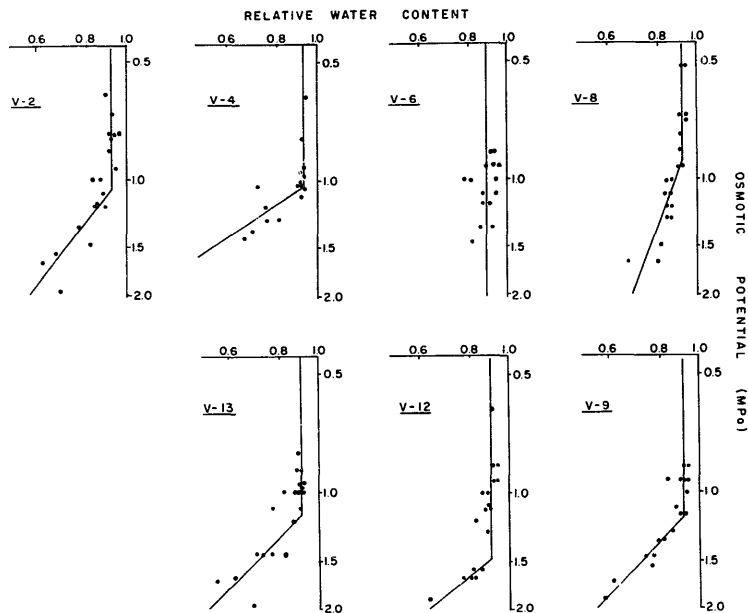


Fig. 2. Relationship between the natural logarithms of relative water contents and the natural logarithms of osmotic potentials, for the seven pea lines, in one dehydration cycle.

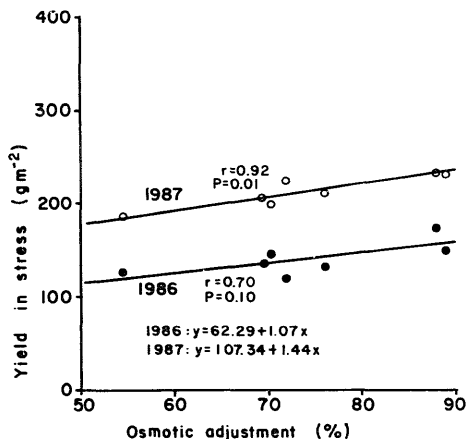


Fig. 3. Correlations between osmotic adjustment and yield of peas in drought conditions.

adjustment. This is not a particularly low OP compared with values measured in plants in the glasshouse or the field. However, it represented fairly severe stress for plants grown under controlled environment conditions.

The regression between yield and osmoregulation was better in 1987 than in 1986. Although rain (during March, April, May and mid June), irrigation and temperature (in May and mid June) were similar in both years (Table 2), the population density in 1987 was about 47% higher than in 1986, this possibly inducing greater stress. This and the fact that the experiment had four replications in 1987, and only two in 1986, are factors that may have influenced the better fit of the regression in 1987. It was not possible to establish a linear regression in 1988 between yield and osmotic adjustment. Although certainly some degree of water stress was produced (positive correlation between yield and irrigation, Fig. 1), it was not enough to result in a positive effect of osmoregulation upon yield.

Pea lines V-6 and V-12 have shown the best osmoregulation capability (Figs. 2 and 3). They have shown too the best yield under stress (mean yield at 12–14 m from the line of sprinklers, in 1986 and 1987), (Fig. 3, Table 2). Furthermore, V-12 showed during the three years (1986, 1987 and 1988) a mean yield (including all the irrigation treatments) that was the highest or at least not significantly different ($P=0.01$) from the highest mean yield (Table 2). The genotype V-12 comes from a cross between V-6 and Filby (semi-leafless), and it has two characteristics associated with drought resistance: a high capacity for osmoregulation and high water-use efficiency because of the semi-leafless character (Rodríguez-Maribona et al., 1990). It therefore seems that osmoregulation may be an important physiological trait to be introduced into future resistant lines.

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