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GAS EXCHANGE IN GREENHOUSE GROWN PEPPER UNDER NITROGEN AND WATER STRESS

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Abstract: This paper reports the results of a trial on greenhouse grown pepper to study the effects of nitrogen and water stress on the major assimilation parameters at the leaf and the crop level and to identify the ones that play a major role on pepper productivity and water use efficiency. Two nitrogen levels (0 and 200 Kg ha⁻¹ of N) factorially combined with two irrigation regimes (restoring every three days 100% of crop water requirements and irrigating whenever the minimum leaf water potential decreased below -2.4 MPa) were compared. At the leaf level, water stress more than nitrogen shortage unfavorably affected assimilation activity. However, the reduction in photosynthesis activity as a result of water stress was less than proportional to the decrease in transpiration rate, whereas the reduced assimilation rates of the unfertilized treatments were associated with a slight increase in the transpiration rate. This entailed a reduction in water use efficiency due to nitrogen shortage and an increase in efficiency due to water stress. At the crop level, the two shortages reduced the leaf area with the resulting reduction in light interception. Therefore, the drop in the assimilation rate at the crop level was, in both cases, higher than the one measured in leaves. The greater adaptation capacity of the crop to water shortage allowed, however, to better compensate the negative effects of this stress, thus reducing the drop in the total dry aboveground biomass with respect to the drop in the assimilation rate in the leaves. In terms of total dry aboveground biomass, this has further improved the crop water use efficiency. Instead, at the crop level, nitrogen shortage has further reduced water efficiency as compared with the leaf.

INTRODUCTION

Photosynthesis is a physiological process by which solar energy is converted into chemical bond energy stored as carbohydrates. This process takes place in the leaf but, following on the translocation and partitioning of photosynthates in the storage organs, it allows the formation of the marketable organs of the plant.

CO₂ flow between the atmosphere and the leaf mesophyll takes place through the stomatal openings; the same path is shared, in the opposite direction, by the water flow generated by transpiration. This accounts for the close association between transpiration and photosynthesis and the great influence exerted by water constraints on the assimilation processes. In fact, if soil available water tends to deplete excessively, the plant reacts, to preserve the soil water storage until the end of its growth cycle, by reducing the transpiration rate through adaptation mechanisms (Turner, 1979), although this inevitably causes a drop in the assimilation activity. However, the photosynthetic capacity greatly varies also among species (Sinclair and Horie, 1989); it depends on a number of factors like the age of the tissue (Connor *et al.*, 1993), the sink assimilate demand (Frageria, 1992) and the availability of water as well as light and nutrients. As for the latter, nitrogen plays a decisive role. In fact, the photosynthetic capacity of leaves is closely related to their content of nitrogen (Connor *et al.*, 1.c.), which is a structural element of chlorophyll but also affects the content of RuBisCo and other carboxylation enzymes involved in the photosynthesis process (Makino *et al.*, 1994). Although, it is not quite clear which of these elements is the major limiting factor of photosynthesis under nitrogen shortage conditions (Marshall and Vos, 1991; Connor *et al.*, 1.c.; Makino *et al.*, 1.c.). This accounts for the unambiguous positive effect, usually reported in literature, of nitrogen fertilization on assimilation processes (Sinclair and Horie, 1.c.). Water and nitrogen shortages influence the productivity of crops also because of the negative effects on the leaf area expansion and duration (Hsiao, 1993;

Frederick and Camberato, 1995) and on the canopy architecture (Pitacco et al., 1990). The interaction of these parameters determines the amount of solar radiation absorbed by the crop and that can thus participate in photosynthesis (Russel *et al.*, 1989). For fully understanding the yield mechanisms and the effects of the constraints induced by the crop environment on yields, the data observed at the leaf level have necessarily to be related to the whole canopy level. This approach is followed in many mechanistic simulation mathematical models of crop growth (Gaudriaan, J., Van Laar, H.H., 1978).

In the last years, numerous basic relationships have been developed to model mathematically the effect of water and nitrogen on the major plant physiological functions, but they are still insufficient to understand the interaction of all the variables involved in the production process. In fact, although the said leaf and crop parameters are only some of those involved in plant physiology, it is evident that, beyond the single response mechanisms, it is rather complicate to draw even theoretical considerations on the interaction between these parameters and their effects on yield. It is then useful to investigate further the field research in order to study and understand the said processes, but also to provide indications and parameters useful for mathematical modeling.

Given the economic importance of pepper in southern Italy and the scarcity of experimental data on this crop, especially when pepper is grown in the greenhouse, the following research was carried out to study the effects of nitrogen and water stress on the major assimilation parameters both at the leaf and at the crop level, and to identify which ones have a predominating importance for pepper productivity and water use efficiency.

MATERIALS AND METHODS

Cropping practices and experimental treatments.

The trial was performed in a conditioned metal and glass house of "Aturia" type at the Faculty of Agriculture of the University of Basilicata; it lies on a sandy loam soil, poor in organic matter and with total nitrogen content of 1.9%. Pepper crop (cv Vidi) was transplanted on May 2 1996 with a density of 2.8 plants m⁻² (arrangement 0.4 x 0.9 m), and scalar harvesting was performed at the stage of the change of color of berries, starting from July 10 until August 27. A system of automatic heating started whenever air temperature dropped below 12°C, whereas the upper opening was performed whenever air temperature exceeded 25°C; average air humidity was almost constant during the whole growth cycle with an average value of 70%. The routine cropping practices were performed during the whole growing cycle; they consisted in hand-made hoeing and phytosanitary treatments against aphids and thrips.

Two nitrogen levels were applied (one treatment receiving 200 nitrogen units as ammonium nitrate, N₂₀₀, fractionated into four applications and an unfertilized one, N₀) combined factorially using a randomized block design with three replications, with two irrigated treatments: one in which - with average three day rotations - the crop water requirements were fully met (WW), and the other in which - from complete rooting on - irrigation was performed whenever the crop exhibited symptoms of water stress (minimum leaf water potential <-2.4 MPa, WS). Water use in the WW treatments was estimated by multiplying reference evapotranspiration measured by an atmometer (ET gage model E) located in the middle of a plot WW by an experimental coefficient taken equal to 1.2. In the WS treatment, following on the adopted criteria, two stress cycles were induced at the end of which a watering volume of 55 mm was applied.

Measurements taken

At the leaf level, on mature leaves well exposed to radiation, starting on June 20 (49 DAT) from 12 a.m. to 1 p.m. solar hours of sunny days, the following was measured on weekly basis:

- The leaf water potential (Ψ_1), using Scholander pressure chamber (mod. PMS);
- Net photosynthesis (A) and transpiration (T_1), through portable gas exchange gage (ADC mod. LCA2);
- Leaf diffusive resistance to gas exchanges (r_s), through a steady type diffusion porometer (LiCor mod. 1600);
- The chlorophyll content a (chl a) and b (chl b) through extraction by dimethylformamide and subsequent spectrophotometric determination (Moran and Porath, 1980).

At the end of the second stress cycle (118 DAT), when the four experimental treatments were definitely differentiated, the curve of the photosynthetic response to light was taken for each treatment by varying the light intensity of Parkinson assimilation chamber between 0 and 3200 μmol of photons $\text{m}^{-2}\text{s}^{-1}$ of photosynthetically active radiation (PAR), using an artificial light source ADC PLU2-002, and keeping the temperature of the cuvette at $34 \pm 0,5^\circ\text{C}$. The data thus obtained were interpolated through an asymptotic exponential function modified for the estimate of the compensation point of photosynthesis:

$$A = A_{\max} (1 - e^{-(\text{PAR} - P_c) \varepsilon / A_{\max}}) \quad (1)$$

where A_{\max} , P_c and ε are, respectively the values of maximum assimilation under light saturation conditions, the compensation point of photosynthesis and the initial quantum yield. At the leaf level, water use efficiency was calculated as a ratio of assimilated CO_2 and the transpiration rate (WUE_1 , $\mu\text{molCO}_2/\text{mmolH}_2\text{O}$).

At the crop level, together with the leaf determinations, measurements were also taken of the incoming photosynthetically active radiation on the crop (PARi), the PAR transmitted to the soil (PART) and reflected by the crop and the bare soil (PARr and PARs) through ceptometers (Decagon mod. SF-80) for the calculation of the PAR absorbed by the crop (PARa) through the following relationship:

$$\text{PARa} = \text{PARi} - \text{PARr} - \text{PART} + \text{PART} (\text{PARs}/\text{PARi})(1 - \text{PART}/\text{PARi}) \quad (2)$$

At the end of the second stress cycle, in all the experimental treatments also the leaf incidence angle with respect to the zenith was measured by a compass-protractor device and the relative values of frequency were interpolated through a beta distribution function (Goel and Strebel, 1984).

During the growth cycle, the leaf area index (LAI) and the total and marketable production, both green and dry, were measured, whereas at the end of the cycle the aboveground total dry matter and the harvest index were determined ($\text{HI} = \text{D.M. berries}/\text{D.M. total}$).

Water consumption in each experimental treatment (ET) was evaluated through the water balance computation. At the crop scale, water use efficiency was calculated as a ratio of total aboveground dry biomass measured in each experimental treatment and the respective water use ($\text{WUE, KG D.M.}/\text{m}^3 \text{ ET}$).

RESULTS AND DISCUSSION

Figure 1 reports the pattern of the leaf water potential (Ψ_1), photosynthesis (A), transpiration (T_i) and stomatal resistance (r_s) measured during the survey period in the four experimental treatments. As it can be observed, the nitrogen shortage didn't affect at all the water status of the crop; in fact, the average Ψ_1 of the measuring period was equal to -1.6 MPa both in treatment N_{200} and in N_0 (table 1).

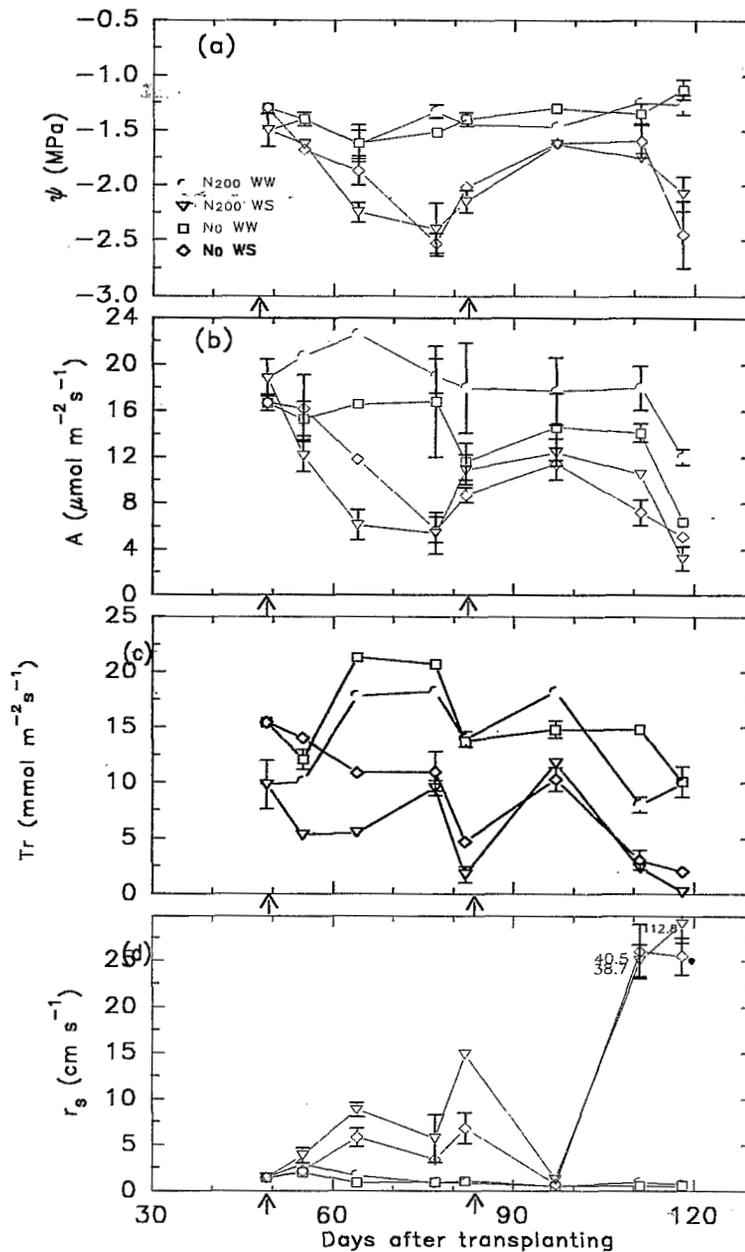


Figure 1. Trends of leaf potential (a), net photosynthesis (b), leaf transpiration (c) and leaf diffusive resistance (d) measured in the four experimental treatments during pepper growing cycle. The arrows indicate the irrigation time in the water stressed treatments (WS). Vertical bars are the standard error of the mean.

Table 1: Average values of the measuring period of leaf water potential (Ψ_l , MPa), net photosynthesis (A , $\mu\text{molCO}_2\text{m}^{-2}\text{s}^{-1}$), transpiration (T_l , $\text{mmolH}_2\text{Om}^{-2}\text{s}^{-1}$), stomatal resistance (r_s , s cm^{-1}) and leaf water use efficiency (WUE_l , $\mu\text{molCO}_2/\text{mmolH}_2\text{O}$). In the lines, the means followed by different letters are significantly different from each other according to Duncan test at $P = 0.01$.

	N Kg ha ⁻¹		Irrigation regime		N x Irrigation regime			
	N ₂₀₀	N ₀	WW	WS	N ₂₀₀ WW	N ₂₀₀ WS	N ₀ WW	N ₀ WS
Ψ_l	-1.6	-1.6	-1.4 A	-1.9 B	-1.4	-1.9	-1.4	-1.9
A	14.0 A	12.0 B	16.1 A	10.1 B	18.2 A	9.9 C	14.1 B	10.3 C
T_l	9.4 B	12.2 A	14.3 A	7.3 B	13.2 A	5.7 C	15.4 A	8.9 B
r_s	12.5 A	6.1 B	1.1 B	17.4 A	1.2 C	23.6 A	0.99 C	11.2 B
WUE_l	1.5 A	1 B	1.1 B	1.4 A	1.4	1.7	0.9	1.2

Instead, a significant effect of soil water shortage was observed in treatments WS, where it caused a progressive lowering of water status of leaf tissues whose potential varied on average between -1.5 MPa under conditions of good soil water storage to -2.4 MPa at the end of the two stress cycles.

Net photosynthesis was significantly reduced as a consequence of both nitrogen and water shortage; the analysis of figure 1 clearly shows the lower assimilation rate generally observed in treatments N₀ and the progressive reduction of photosynthetic activity as water stress advances in treatments WS. On average, nitrogen shortage reduced A by 14% (14.0 and 12.0 $\mu\text{molCO}_2\text{m}^{-2}\text{s}^{-1}$ as an average of treatments N₂₀₀ and N₀, table 1) whereas the water stress by 37% (16.1 and 10.1 $\mu\text{molCO}_2\text{m}^{-2}\text{s}^{-1}$ as an average of treatments WW and WS, table 1).

From the analysis of the interaction of the two factors, it is evident also that water shortage caused a greater drop in assimilation (46%) in more fertilized plots (18.2 and 9.9 $\mu\text{molCO}_2\text{m}^{-2}\text{s}^{-1}$ measured in treatments N₂₀₀WW and N₂₀₀WS, table 1).

From the analysis in figure 2 and table 2, illustrating the functions and the relative parameters of the photosynthetic response to light, clear variations are evident of the functionality of the photosynthetic system versus nitrogen and water shortage. A max was reduced on average by 20% due to the lack of nitrogen supply (11.8 and 9.4 $\mu\text{molCO}_2\text{m}^{-2}\text{s}^{-1}$ as an average of treatments N₂₀₀ and N₀, tab. 2) and by 85% due to water stress (18.5 and 2.7 $\mu\text{mol CO}_2 \text{m}^{-2}\text{s}^{-1}$ as an average of treatments WW and WS, table 2).

Although the said functions were calculated at the time of peak water stress in treatments WS, this is indicative of the severe effects that water stress generally causes on the assimilation capacity of leaf tissues.

In particular, the greatly reduced assimilation capacity in treatments WS is to be related to the almost complete stomatal closure upon measurements ($r_s > 20 \text{ s cm}^{-1}$, fig. 2); this confirms and explains, as previously said and evident also in figure 1, the close association between the reduction in the opening degree of stomata and the drop in A and T_l .

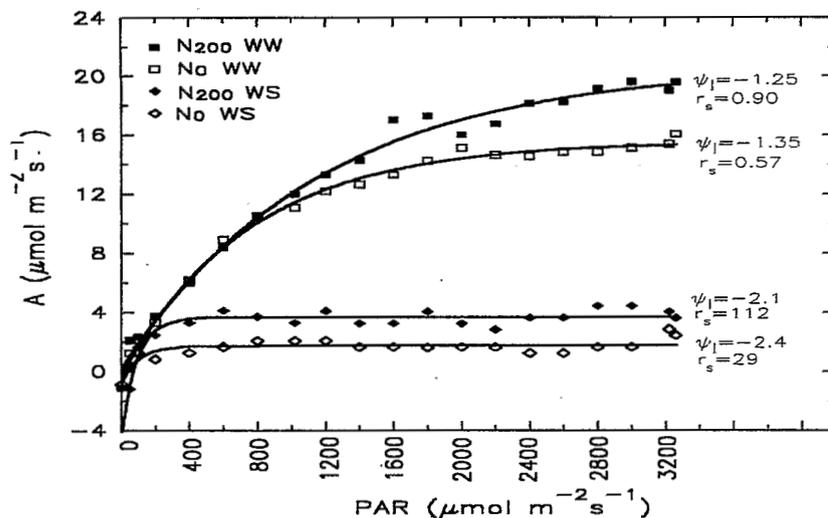


Figure 2. Response curves of net photosynthesis (A) of pepper leaves to photosynthetically active radiation (PAR). On the right of each curve, the leaf water potential (Ψ_1) and the leaf diffusive resistance (r_s) of adjacent leaf is reported

Table 2: Effects of nitrogen and water stress on maximum assimilation (A_{max} , $\mu\text{molCO}_2\text{m}^{-2}\text{s}^{-1}$), compensation point (P_c , $\mu\text{molPARm}^{-2}\text{s}^{-1}$), initial photosynthetic efficiency (ε , $\mu\text{molCO}_2\mu\text{molPAR}^{-1}$), average content of chlorophyll a and chlorophyll b ($chl\ a+b$, mgm^{-2}) and ratio of chlorophyll a to b ($chl\ a/b$). In the lines, the means followed by different letters are significantly different from each other according to Duncan test at $P=0,01$ (capital letters) and $P=0.05$ (small letters).

	N Kg ha ⁻¹		Irrigation regime		N x Irrigation regime			
	N ₂₀₀	N ₀	WW	WS	N ₂₀₀ WW	N ₂₀₀ WS	N ₀ WW	N ₀ WS
A_{max}	11.8 A	9.4 B	18.5 A	2.7 B	20.7 A	3.7 C	15.5 B	1.7 C
P_c	39.8	22.2	11	51.1	11.1	68.6	10.9	33.6
ε	0.029	0.019	0.019	0.029	0.018	0.041	0.021	0.017
$chl\ a+b$	572.4 A	429.1 B	472.3 b	529.2 a	558.7	586.2	386.0	472.3
$chl\ a/b$	3.3	3.5	3.4	3.3	3.3	3.3	3.6	3.4

The higher assimilation capacity observed in the treatment with a greater availability of nitrogen is, instead, to be attributed both to the greater activity of RuBisCo, and to the higher efficiency of enzymatic systems of Calvin cycle and carboxylase processes (Tei *et al.*, 1993), in addition to the greater chlorophyll content. In fact, as for the latter, the average values of chlorophyll content measured during the cycle was, per unit surface, by 33% greater in treatments N₂₀₀ with respect to N₀ (table 2). The nitrogen dose and the irrigation regime didn't affect the initial quantum yield (ε , table 2); this is understandable in that at low irradiance, photosynthesis is limited by the energy input rather than the carboxylase activity or by the diffusive stomatal resistance to gas exchanges. Equally negligible was the effect of the two factors under study on the compensation point for CO₂, that was on average equal to 31 $\mu\text{molPARm}^{-2}\text{s}^{-1}$, and on the ratio of chlorophyll a to b (table 2) indicating that at the stress levels attained in the trial the functionality of the two photosystems was not affected (Tei *et al.*, 1.c.).

As it was to be expected, and for the reasons discussed above, a marked effect of the irrigation regime on the transpiration rate (T_i) was observed; as from figure 1, in treatment WS the latter progressively decreased as stress increased. In the said treatment, this caused an average reduction of 49% of T_i with respect to WW (tab. 1). It is interesting to note that because of stomatal closure, the reduction in the photosynthetic activity (34%, table 1) was less than proportional to the drop in transpiration, in agreement with the theory of leaf gas exchanges (Jones, 1976); this has important effects on the water use efficiency. Nitrogen shortage has caused a small increase in transpiration activity (22%, table 1), consistently related to the lesser stomatal resistance observed on average in treatment N_0 with respect to N_{200} (respectively 6.1 and 12.5 $s\ cm^{-1}$, table 1).

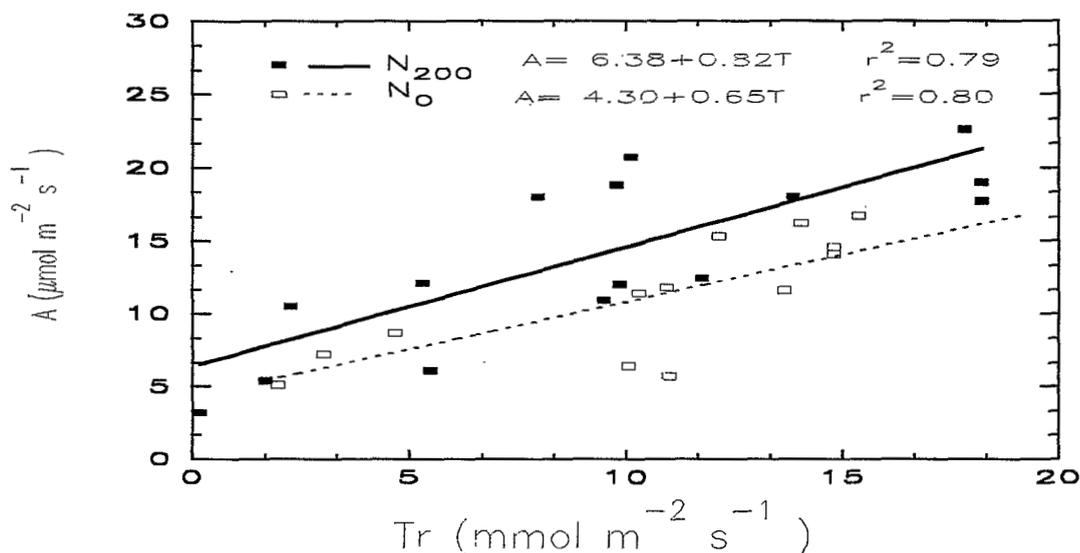


Figure 3. Relation between leaf net photosynthesis (A) and leaf transpiration (T_r) measured on pepper subject t , the two levels of nitrogen application ($N_{200} = 200\ kg\ ha^{-1}$ of N, $N_0 = 0\ kg\ ha^{-1}$ of N)

The combined analysis of transpiration and leaf photosynthesis data reported in figure 3, showed that, the transpiration rate being the same, the greater availability of nitrogen provoked a significant increase in assimilation processes; this, in turn, determined an increase in the water use efficiency of fertilized treatments, that moved from 1.0 $\mu molCO_2/mm olH_2O$ of treatments N_0 to 1.5 $\mu molCO_2/mm olH_2O$ of treatments N_{200} (WUE_1 , table 1). For the above said reasons, it was water shortage to cause an increase in WUE_1 , that moved from 1.1 $\mu molCO_2/mm olH_2O$ of treatments WW to 1.4 $\mu molCO_2/mm olH_2O$ of treatments WS (table 1). Consequently, the highest efficiency levels were obtained in treatments $N_{200}WS$ (1.7 $\mu molCO_2/mm olH_2O$, table 1), whereas the lowest ones in treatments N_0WW (0.9 $\mu molCO_2/mm olH_2O$, table 1).

Moving now to examine the data collected at the crop scale (table 3), it is evident that nitrogen shortage has, on average, reduced the maximum LAI by 56% (1.6 and 0.7 respectively in N_{200} and N_0 table 3), whereas water stress reduced it by 32% (1.4 and 0.95 respectively in WW and WS, table 3).

Table 3 : Effects of nitrogen and water stress on the maximum leaf area index (LAI_{max}), on absorbance ($Abs. = PAR_a/PAR_i$), on the total aboveground dry matter ($D.M., g\ m^{-2}$), on water use efficiency ($WUE, Kg\ D.M./m^3\ ET$), on harvest index ($H.I.$) and on marketable yield ($M.Y., t\ ha^{-1}$).

	N Kg ha ⁻¹		Irrigation regime		N x Irrigation regime			
	N ₂₀₀	N ₀	WW	WS	N ₂₀₀ WW	N ₂₀₀ WS	N ₀ WW	N ₀ S
LAI_{max}	1.6 A	0.7 B	1.4 a	0.95 b	1.9	1.3	0.9	0.6
$Abs.$	0.50 A	0.30 B	0.50 A	0.30 B	0.59	0.41	0.41	0.20
$D.M.$	446 A	235 B	432 a	249 b	531	362	334	137
WUE	1.30 A	0.63 B	0.77 B	1.18 A	0.95 b	1.70 a	0.60 b	0.66 b
$H.I.$	0.44	0.47	0.53 A	0.38 B	0.51	0.38	0.56	0.39
$C.Y.$	20.4 A	14.4 B	25.2 A	9.6 B	28.0	12.8	22.5	6.4

In the lines, the means followed by different letters are significantly different from each other according to Duncan test at $P = 0.01$ (capital letters) and $P = 0.05$ (small letters).

As shown by the absorbance data ($Abs. = PAR_a/PAR_i$, table 3), this caused a reduction in the capacity of the crop to intercept and absorb radiation to be used in the photosynthesis process; similarly for the two shortage conditions, absorbance decreased from 0.50 to 0.30. The fact that despite a smaller percentage reduction of the leaf area in the water stressed treatments with respect to the nitrogen stressed ones, an identical drop in absorbance was evident in both, is attributable to the modified architecture of the canopy observed only in treatments WS.

As it is observed in figure 4, water stress has considerably modified the distribution of the leaf angles, moving the mode of beta function from an angle of incidence of about 90° of treatments WW to about 20° of WS; these variations are well in agreement with those observed on the same species by Pitacco (l.c.) under field conditions and, for reasons related to the energy balance, they participate in limiting crop transpiration under stress conditions (Hsiao, 1990). However, this also means an advantage in the use of the limited water resource since the lower assimilation rates observed under water stress conditions are compensated not only by the increased leaf WUE but also by a further reduction in the transpiration rate of the whole canopy.

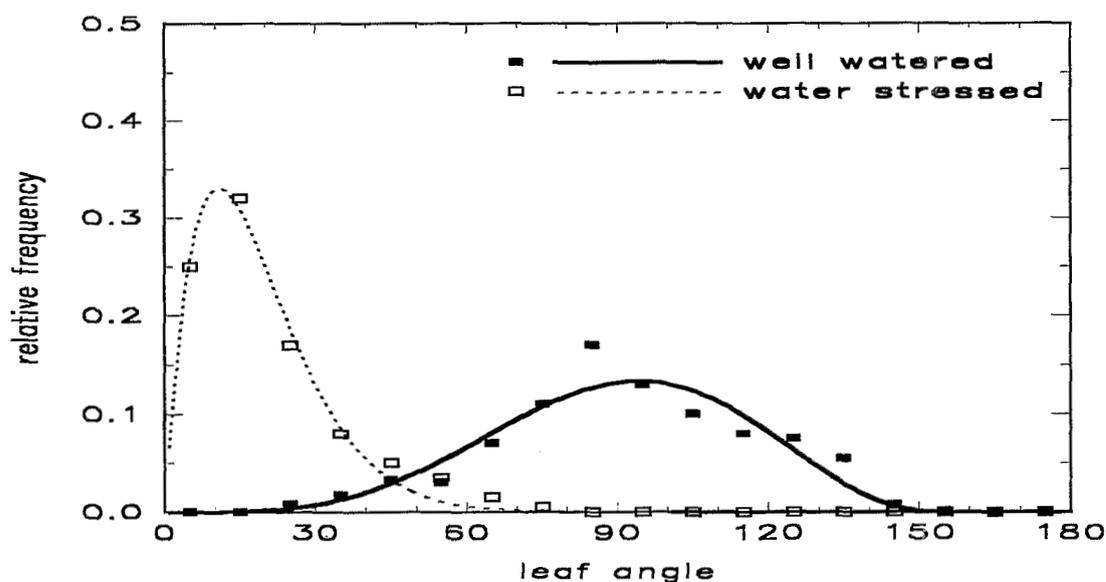


Figure.4 Leaf angle frequency distribution measured on pepper subject to the two irrigation regimes

Nitrogen shortage depressed by 47% the total aboveground dry matter (446 and 235 g m⁻² respectively in treatments N₂₀₀ and N₀, table 3) whereas water stress reduced it by 42% (432 and 249 g m⁻² respectively in treatments WW and WS, table 3). As it can be noticed, the assimilation reduction at the crop level was, for both shortage conditions, greater than the one observed at the leaf level, since the effect of the reduced photosynthetic capacity added up to the effect of the reduced leaf area. It is interesting to notice also that at the canopy scale, as compared with the leaf scale, nitrogen shortage has affected crop productivity more than water shortage. In fact, the D.M. was reduced by 47% with respect to a 14% drop of A moving from N₂₀₀ to N₀, whereas the D.M. decreased by 42% with respect to a 37% drop of A moving from WW to WS. This would seem to indicate that at the crop level, the mechanisms of adaptation to water stress acted more strongly than the adaptation to water stress observed at the leaf level. Contrary to what observed on A at the leaf level (table 1), the analysis of variance didn't show a significant interaction between the two factors under study (table 3). Therefore, with respect to the aboveground dry matter obtained from treatments N₂₀₀WW of 531 g m⁻², the nitrogen shortage has reduced the D.M. to 334 g m⁻², the water stress reduced it to 362 g m⁻² and the negative effects of the two shortages simply added up thus reducing the D.M. to 137 g m⁻² in treatments N₀WS.

The crop adaptation to water shortage had notable effects also on WUE that, at the crop level, was depressed by 51% because of the nitrogen shortage (1.3 and 0.63 Kg D.M. m⁻³ ET respectively in N₂₀₀ and N₀, table 3) with respect to a 33% drop at the leaf level; instead, water shortage at the crop level has improved the WUE by 53% (0.77 and 1.18 Kg D.M. m⁻³ ET respectively in WW and WS, tab. 3) with respect to an increase of 27% observed at the leaf level (table 2); therefore, in terms of water resource use efficiency, the highest levels were attained in the fertilized and water stressed treatment (1.7 Kg D.M. m⁻³ ET, table 3) whereas the lowest ones in the unfertilized and well irrigated treatments (0.6 Kg D.M. m⁻³ ET, table 3).

However, water shortage significantly reduced the harvest index (that decreased on average from 0.53 in treatments WW to 0.39 in treatments WS, table 3), because of the abscission of fruitlets and the affected fruit-setting; this becomes clear if one considers that water stress occurred during most of the reproductive stage, and accounts for the greater reduction in pepper yield as compared with the total biomass, as often reported in literature under similar conditions (Hsiao *et al.*, 1976). In fact, the yield reduction of marketable berries was of 60% in WS treatments with respect to WW ones (table 3), and thus quite greater than the one observed on total dry matter. So, although in terms of total biomass the crop showed good adaptation capacities to water stress, the modified partitioning of assimilates, strongly affected the yielding capacity of this species.

CONCLUSIONS

The results obtained in a trial on greenhouse grown pepper, in order to study the effects of water and nitrogen shortages on the assimilation parameters both at the leaf and crop level, and to identify the ones that play a decisive role on pepper productivity and water use efficiency, gave the following indications:

- At the leaf scale, water stress more than nitrogen shortage negatively affected the assimilation capacity; water stress affected photosynthesis because of the stomatal closure whereas nitrogen shortage affected it because of the smaller concentration in chlorophyll and the reduced enzymatic activity. However, the reduction in the photosynthetic activity resulting from water stress was less than proportional to the drop in transpiration, whereas the reduced assimilation rates observed in unfertilized treatments was associated with a slight increase in the transpiration rate. This entailed a reduction in the water use efficiency due to nitrogen shortage and an increase in efficiency due to water stress.

- At the crop scale, the two shortages reduced the leaf area and, consequently, the light interception. Then, the drop in the assimilation rate observed at the crop level was, for both shortage conditions, greater than the one observed at the leaf level, since the effect of the reduced photosynthetic capacity added up to the effect of the reduced leaf area. The greater adaptation capacity of the crop to water shortage allowed, however, to compensate better the negative effects of this stress, thus reducing the drop in the aboveground biomass with respect to the assimilation one observed in leaves. This has further improved the water use efficiency observed at the crop level with respect to the one measured at the leaf level. Referring again to the whole crop, nitrogen shortage, instead, further reduced water efficiency as compared with the leaf. It should equally be noticed that water stress, by reducing also the harvest index, greatly reduced the berry yield thus affecting the good adaptation capacity the crop had shown in terms of total biomass.

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