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Gas exchange characteristics, water use efficiency and osmotic adjustment in relation to heterosis in hot pepper (*Capsicum annuum* L.) under water stress

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Abstract: Two hybrids and parents (hyb MSH-11; IHR 3289 male, IHR 3285 female and hyb ECH-86; IHR 2444 male, IHR AR 18 female parents) of hot pepper (*Capsicum annuum* L) were studied to examine the response of morphological attributes, net photosynthetic rate (P_N), stomatal conductance (g_s) and water use efficiency (WUE) under control (irrigated) and water stress conditions. Water stress was imposed at flowering stage under field condition by withholding the irrigation for a period of 35 days. Both the hybrids responded differentially to water stress. In general, the plant height, fruit numbers, fruit fresh weight and total dry matter (TDM) accumulation were higher in hybs than their respective parents in control as well as stress conditions. The fruit bearing and TDM accumulation were more in hyb MSH-11 compared to the hyb ECH-86. The hyb ECH-86 had the higher P_N compared to parents under control as well as stress conditions. However, in hyb MSH-11, there was no definite patter in P_N under control but it was greater than parents under water stress. Though, in both the hybs P_N decreased substantially after 21 days of stress, the quantum of decrease was more in hyb ECH-86 than hyb MSH-11. Further MSH-11 had shown better osmotic adjustment (OA) than hyb ECH-86. The higher WUE of hyb MSH-11 than its parents under control and stress conditions shows the heterosis for WUE in this hybrid. WUE was higher in hyb MSH-11 (2.5µ mol CO_2/mol H_2O) as compared to hyb ECH-86 (2.0µ mol CO_2/mol H_2O) under stress which may be due to the higher P_N in this hybrid under stress. The heterosis for TDM, P_N and WUE in hyb MSH-11 under stress may be a contributing factor for better performance of this hyb under stress.

Keywords: Gas exchange, water use efficiency, hot pepper

Introduction

Soil water deficit is one of the major environmental factors limiting crop growth, yield and quality worldwide, especially in the tropical areas. Different approaches under genetic improvement have been followed in improving the adaptability of the crop plants to the tropical conditions. Efforts have been made to develop the hybrids (hybs) perform better under the normal as well as water stress conditions (Hoffman *et al*., 1984; Khana-Chopra and Sinha 1993; Gangadhar *et al*., 1999). The better performance of hybs under water stress was associated to the heterosis in physiological parameters (Blum 1983; Gangadhar *et al*., 1999). Mojayad and Planchon (1994) reported that the P_N performance and its adjustment appears to be closely associated with heterosis which can develop a tolerance to internal water deficit in hybs. The expression of heterosis under water limited environment has been reported mainly in cereal crops (Hoffman *et al*., 1984, 1993; Gangadhar *et al*., 1999). However, there is not adequate information about the heterosis expression in horticultural crops such as hot pepper in relation to water stress. Although, hot pepper (*Capsicum annuum* L.) is grown widely in India, drought combine with high temperature limits its yield potential in the tropics. Under crop improvement programme efforts have been initiated at this institute in improving the adaptability of hot pepper under rain fed conditions. Studies of the drought response of hybs and their parents offer an opportunity for an improved understanding of the genetic and physiological basis of adaptation to water stress. A study was, therefore, carried out to evaluate the physiological parameters that confer tolerance to water stress in hybs of hot-pepper.

Materials and Methods

Plant material and growth conditions: The study was conducted on two hybs and parents (hyb MSH-11 and IHR 3289 male and IHR 3285 female parents; hyb ECH-86 and IHR 2444 male and AR18 female parents) of

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hot pepper (C*apsicum annuum* L). Hyb MSH-11 had tall plants with long fruits, while hyb ECH-86 was short stature well branched with larger fruit size. The seedlings of hybs and their parents were raised in a nursery. Four weeks old uniform seedlings were transplanted in the field in a split plot design with three replications during summer season. After transplanting, the plants were regularly irrigated to field capacity until flower bud formation (45 days from transplanting). Water stress was imposed at flowering stage in one set of plants for a period of 35 days by withholding irrigation (stress). Another set was irrigated regularly (control). During the stress period, observations were made on the morpho-physiological parameters.

Morphological parameters

Plant height, total leaf area, number of branches, fruit number, fruit fresh weight and total plant dry weight were taken before and at 30 days after releasing stress. The LA of the plant was measured using Leaf area meter (LI-3000). The plant parts were separated and dried in an oven at 80 ^{0}C for 72 h to calculate the total dry matter (TDM) of individual plant.

Gas exchange parameters

The observations on net photosynthesis (P_N), transpiration rate (E), stomatal conductance (g_s), were recorded at 7 days interval on the fully expanded leaf using portable photosynthetic system model LCA-3 (*Analytical Development Corporation*, UK). The day temperature varied from 29 to 32 ^{0}C, irradiance varied from 1200 to 1400 µmol m^{-2} s^{-1} (PAR) and the CO_2 concentration was 350 cm^3 m^{-3} during the observations. All the observations were recorded between 10.00 am and 11.30 am. Water use efficiency (WUE) was calculated from CO_2 exchange rate and transpiration expressed as µmol CO_2/mol H_2O.

Plant water relation

A portion of the leaf used for photosynthetic determination was frozen for a week, thawed and sap was used for osmotic potential ($Ø_S$) determination in a vapor pressure osmometer (Wescor 5100C, USA). Osmotic adjustment (OA) was calculated as the difference in $Ø_S$ at full pressure potential between control and stress treatments (Blum 1989).

Statistical analysis

Statistical analysis was done by computing the standard deviation and analysis of variance (ANOVA) at 0.05 levels of probability.

Results

Morphological parameters

The response of morphological parameters of both the hybrids and their parents under control and stress conditions were shown in Table 1. The plant height in both the hybs was more than their male parents but less than the female parents under control as well as stress conditions (Table 1). The number of branch were in hyb MSH-11 were higher than its parents under both the conditions while in ECH-86 the number of branches were more than its parents under control. The fruit number under both the conditions were found greater in the hybs than their parents. The LA production was higher in hyb ECH-86 than its parents in control as well as stress condition, while in hybrid MSH-11, the leaf area was higher than both the parents under stress but lesser than its female parent under control condition. The Specific leaf weight (SLW) has increased under stress, though the increase was non-significant in both the hybrids and parents. The TDM production was greater in hybrids than their parents under both the conditions (Table 1).

After 30 days of relieving stress, there was slight increase in plant height in both the hybrids and maintained the superiority over their respective parents in terms of fruit number, fruit fresh weight and TDM (Table 1). Both the hybrids and their parents have shown recovery of the plant morphological parameters after releasing stress. The hybrid MSH-11 responded better in its recovery as indicated by higher fruit bearing and TDM accumulation than hybrid ECH-86 after releasing stress.

Leaf osmotic potential ($Ø_S$) net Photosynthesis (P_N) and stomatal conductance (g_s)

The leaf $Ø_S$ under control in hyb. MSH-11 and the parents ranged from -1.2 to -1.3 MPa, while in ECH-86 and parents it varied from -1.2 to -1.4 MPa (Table 3). There was a significant decrease in $Ø_S$ in stress plants and it decreased to -2.0 MPa in MSH-11 and to -1.9 MPa in ECH-86. The decrease in $Ø_S$ during stress was more in the male parent (-2.4 MPa) than the female parent (-1.8 MPa) of MSH-11, while in both the parents of ECH-86 the decrease was of the same level (-2.2 MPa)

The pattern of net P_N and g_s in hybs and the parents under control and stress conditions was shown in fig 1a and 1b. There was no significant difference between the hybs and their parents under control but the hybs had higher P_N than the parents. However, under stress

Table 1. Plant height, leaf area, number of branches, number of fruits, total dry matter and specific leaf weight of hot pepper hybrids and their parents under control and stress conditions

Hybrids/parents	35 days stress		30 days after releasing stress	
	Control	Stress	Control	Stress
	Plant height (cm)			
MSH-11	79.0	70.5	88.5	95.0
IHR 3289 (male)	67.5	65.0	87.5	82.5
IHR 3285 (female)	88.0	82.5	110.0	105.0
CD (0.05) treatments	12.19	9.95	9.10	7.43
ECH-86	80.5	65.5	72.5	73.5
IHR 2444 (male)	50.5	46.5	59.0	52.5
IHR AR18 (female)	73.0	72.0	76.0	86.0
CD (0.05) treatments	5.96	4.86	10.75	8.77
	Number of branches			
MSH-11	11.5	11.0	10.5	9.5
IHR 3289 (male)	6.5	7.5	9.5	9.0
IHR 3285 (female)	9.5	7.5	8.0	9.0
CD (0.05) treatments	2.86	2.34	1.77	1.45
ECH-86	7.2	7.0	8.5	7.5
IHR 2444 (male)	5.5	7.1	6.5	6.5
IHR AR18 (female)	6.5	8.5	8.0	7.0
CD (0.05) treatments	2.83	2.31	2.10	1.71
	Number of fruits			
MSH-11	172.5	102.0	273.5	262.5
IHR 3289 (male)	125.5	78.0	189.0	212.5
IHR 3285 (female)	19.5	11.8	46.5	56.5
CD (0.05) treatments	30.09	24.57	50.85	41.52
ECH-86	150.0	66.5	213.0	151.5
IHR 2444 (male)	71.0	55.0	82.5	54.5
IHR AR18 (female)	85.5	57.0	243.0	198.0
CD (0.05) treatments	33.83	27.62	72.71	59.37
	Leaf area (cm^2)			
MSH-11	7385.0	6613.5	7474.0	18945.0
IHR 3289 (male)	4011.0	3350.5	8060.5	11266.5
IHR 3285 (female)	8829.0	6014.5	16619.5	17895.5
CD (0.05) treatments	2079.11	1697.59	4269.51	3486.04
ECH-86	5697.5	3697.5	7145.5	8527.5
IHR 2444 (male)	2697.5	2178.5	2609.0	3664.0
IHR AR18 (female)	2526.5	2448.5	5396.0	6891.0
CD (0.05) treatments	1452.07	1185.61	4187.55	3419.12
	Total dry matter (g $plant^{-1}$)			
MSH-11	147.5	127.0	244.5	337.0
IHR 3289 (male)	87.5	62.0	249.5	240.5
IHR 3285 (female)	132.0	91.5	301.5	335.5
CD (0.05) treatments	12.21	9.97	64.49	52.66
ECH-86	143.0	89.0	210.5	211.5
IHR 2444 (male)	84.5	69.0	132.5	84.0
IHR AR18 (female)	69.5	55.5	166.3	149.5
CD (0.05) treatments	20.02	16.35	69.01	56.35
	Specific leaf weight (mg cm^{-2})			
MSH-11	4.35	5.55	5.60	4.68
IHR 3289 (male)	4.60	5.25	5.80	6.13
IHR 3285 (female)	4.50	5.05	5.30	6.49
CD (0.05) treatments	0.91	0.74	0.33	0.27
ECH-86	5.00	5.55	6.40	5.43
IHR 2444 (male)	5.20	7.80	5.76	5.42
IHR AR18 (female)	6.45	6.25	6.16	5.40
CD (0.05) treatments	3.57	2.92	2.43	1.99

the hybs and the parents responded differentially. In both the hybs and the parents there was a gradual decrease in P_N rate with increasing stress till 21 days stress and thereafter there was a sharp decrease in P_N rate. In hyb MSH-11, the P_N rate reduced to 9.0 µmol m^{-2} s^{-1} and its male and female parents reduced to 7.0 and 7.5 µmol m^{-2} s^{-1}, respectively. In hyb ECH-86, the P_N in decreased to 8.5 µmol m^{-2} s^{-1} and in its male and female parent to 6.5 and 6.0 µmol m^{-2} s^{-1} under stress. No definite pattern of g_s in both the hybrids and their parents was found in control plants. However, there was considerable decrease in g_s after 21 days stress in both the hybs and parents. In both the hybrids, the g_s was greater than the parents at 35 days stress (Table 2). In MSH-11 the decrease in g_s was gradual under stress, while in ECH-86 and its parents there was a sharp decrease with increasing the stress.

Water use efficiency (WUE)

In hyb HSH-11, the WUE was relatively higher as compared to its parents under both control and stress conditions (Fig.2). The Hyb ECH-86 and its male parent (IHR 2444) had almost the same WUE under control.

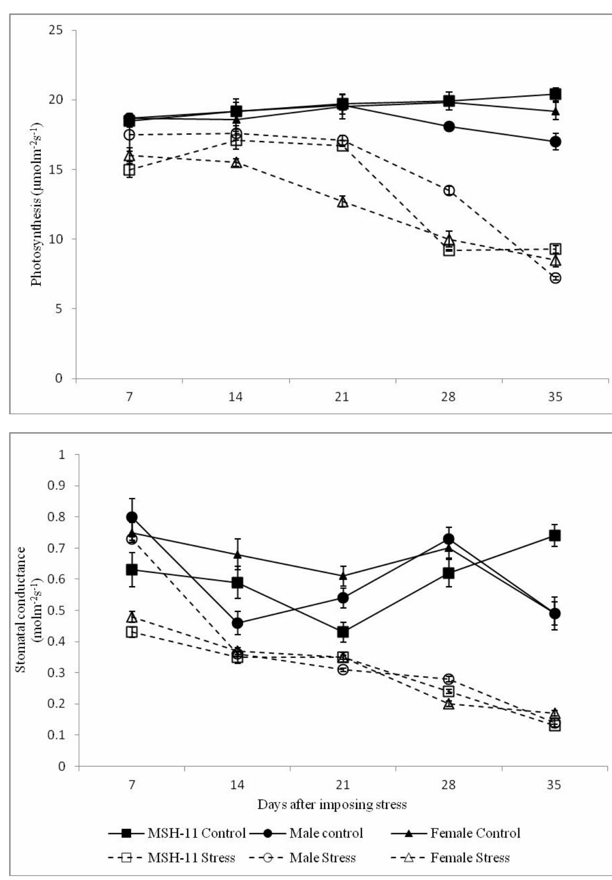

Fig. 1a. Photosynthesis and stomatal conductance response of hybrid MSH-11 and its parents to water stress (bar indicating SEm)

Table 2. Net photosynthesis (P_N), stomatal conductance (g_s) and intercellular carbon dioxide (Ci) in the leaves of hot pepper hybrids and their parents at 35 days stress.

Hybrids/parents	35 days stress		30 days after releasing stress	
	Control	Stress	Control	Stress
P_N (µ molm^{-2}s^{-1}) net photosynthesis				
MSH-11	20.4	9.3	15.6	15.6
IHR 3289 (male)	16.8	7.2	13.5	13.9
IHR 3285 (female)	16.4	8.5	9.8	12.4
CD(0.05)	1.99	1.62	2.71	2.21
ECH-86	19.8	8.5	15.7	12.8
IHR 2444 (male)	18.4	6.5	14.9	9.5
IHR AR18 (female)	16.9	6.1	12.5	10.0
CD(0.05)	2.57	2.10	1.44	1.18
g_s (molm^{-2}s^{-1}) stomatal conductance				
MSH-11	0.70	0.15	0.58	0.29
IHR 3289 (male)	0.49	0.13	0.57	0.57
IHR 3285 (female)	0.48	0.17	0.32	0.38
CD(0.05)	0.15	0.12	0.12	0.10
ECH-86	0.54	0.13	0.32	0.54
IHR 2444 (male)	0.67	0.13	0.41	0.58
IHR AR18 (female)	0.65	0.12	0.33	0.41
CD(0.05)	0.18	0.15	0.11	0.09
Ci (ppm) intercellular				
MSH-11	235	243	289	257
IHR 3289 (male)	275	240	263	267
IHR 3285 (female)	232	233	262	255
CD(0.05)	32.50	26.54	14.11	11.52
ECH-86	235	239	251	267
IHR 2444 (male)	243	245	241	291
IHR AR18 (female)	255	235	243	276
CD(0.05)	26.37	21.53	10.99	8.98

But under stress condition, hyb ECH86 had the higher WUE compared to its both the parents. Among the hybrids, MSH-11 had the greater WUE (3.1µ mol CO_2/ mol H_2O) as compared to hyb ECH-86 (2.7µ mol CO_2/ mol H_2O) under stress.

Discussion

The results indicated that two hybs of hot pepper had shown differential response to water stress. Although in both the hybs there was a reduction in LA under stress, it was greater in ECH-86 (35%) as compared to MSH-11 (10%). In the parents of ECH-86, the reduction under stress was 17.4% in male and 3.0% in female, while in the parents of MSH-11 it was 16.4% in male and 31.8. The greater reduction in LA in ECH-86 may be due to the higher leaf senescence (data not shown) during stress. The leaf senescence and the decrease in leaf growth of the plant are associated to the reduction in LA under drought stress. In the present study, the leaf senescence was found to be more in hyb ECH-86 during stress (data not shown) and this may be a major contributing factor for the higher percentage of LA reduction in this hyb under stress. Further, hyb ECH-86 had the higher percentage of LA reduction than parents, while hyb MSH-11 had the lower percentage of LA reduction than parents under stress indicating differential leaf response to water stress in these two hybs. Although, reduction of leaf growth and narrowing of leaves under water stress considered as an adaptive trait (Blum 1983), as it may help in adjusting its transpiring surface area during stress, the development and maintenance of optimum LA in crop species is the main yield-determining factor under water stress (Fisher and Turner 1978).

However, both the hybrids along with the parents have shown LA recovery potential after relieving the stress as indicated by 80.0% more LA than control in MSH-11 and 36.0% in its male and 7.0% in female parent at 30 days after releasing stress. In ECH-86 and its male and female parents the LA was 19.0, 4.0 and 19.0 % more than control at 30 days after releasing stress. The higher LA recovery in MSH-11 (80.0%) compared to hyb. ECH-86 (19.0%) after 30 days releasing stress indicates the better recovery potential in this hyb.

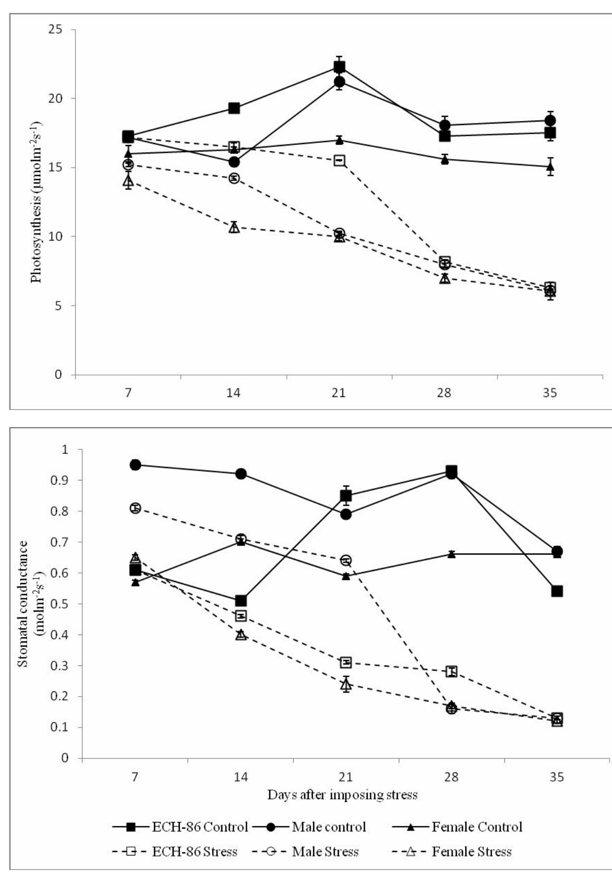

Fig. 1b. Photosynthesis and stomatal conductance response of hybrid ECH-86 and its parents to water stress (bar indicating SEm)

Table 3. Leaf osmotic potential (-MPa) and osmotic adjustment (MPa) in hot pepper hybrids and their parents at 35 days stress

Hybrid/Parent		Osmotic Potential (-MPa) Control	Stress	Osmotic adjustment
MSH – 11		1.2	2.0	0.8
IHR 3289 (Male)		1.3	2.4	1.1
IHR 3285 (Female)		1.3	1.8	0.5
		Genotypes	Treatments	
SEm	0.019	0.015	SEm	0.045
CD(0.05)	0.059	0.048	CD(0.05)	0.177
ECH – 86		1.3	1.9	0.6
IHR 2444 (Male)		1.4	2.2	1.0
AR 18 (Female)		1.2	2.2	0.8
		Genotypes	Treatments	
SEm	0.027	0.022	SEm	0.080
CD(0.05)	0.084	0.069	CD(0.05)	0.316

The higher TDM production by both the hybs as compared to the parents under both the irrigated and water stress conditions indicated the heterosis for biomass production in these two hybs (Table 1). In other crop like sorghum, heterosis for biomass, grain yield and grain number per panicle was reported under rain fed conditions (Gangadhar *et al.*, 1999). The higher SLW under water stress may be due the accumulation of photoassimilate in leaf as during drought stress the photoassimilates are retained at the source leaf (Srinivasa Rao and Bhatt 1992). The study indicates that, in general, both the hybs have heterosis for P_N rate under both the conditions as indicated by higher P_N rate than parents under control and stress conditions. Though, there are the reports on the heterosis for stomatal and photosynthetic adjustment under limited water conditions in hyb sunflower (Mojayad and Planchon 1994), we did not found heterosis for g_s in both the hybs under control as well as water stress. The higher reduction in P_N rate in hyb ECH-86 under stress compared to hyb MSH-11 indicates photosynthetic sensitivity of ECH-86 to water stress. The decrease in g_s may result in a decrease in P_N rate under water stress (fig.1a and 1b). The reduction in g_s was relatively more in hybrid ECH-86 and its parents compared to hybrid MSH-11 and its parents. The reduction in g_s may results in a decrease in CO_2 availability in the mesophyll (Cornic 1994). However, the contribution of non-stomatal regulation of photosynthesis in both the hybs under stress can not be ruled out. The non-stomatal reduction in photosynthesis may be due to decrease in RuBP (ribulose biphosphate synthesis (Gimenez *et al.*, 1992) or decrease in carboxylation efficiency (Martin B and Ruiz-torres NA 1992) or both (Faver *et al.*, 1996). Osmotic potential was more negative in hyb MSH-11 at the end of 35 days water stress than the hybrid ECH-86. There was variation in OA in hybrids and parents. Male parent of both the hybrids had higher OA compared to female parent.

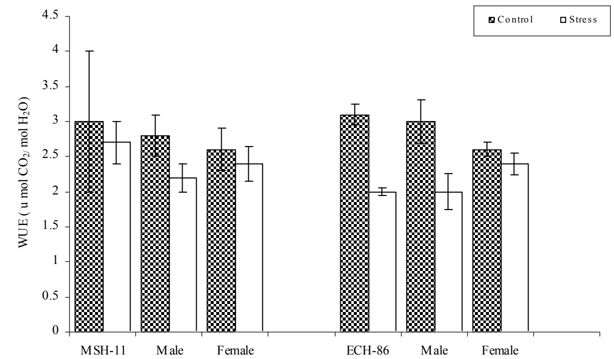

Fig. 2. Water use efficiency of hot pepper hybrids and their parents (bar indicating SEm)

The water stress induced OA differences among the genotypes may be an important attribute of drought resistance (Morgan 1984). Among many physiological parameters responsible for tolerance of plants to water stress, OA is significant in regulating cellular metabolic activities in plants by maintaining pressure potential (Morgan 1992; Serraj and Sinclair 2002). OA adjustment is regarded as a major mechanism of stomatal and photosynthetic adjustment (Turner NC and Jones MM 1980; Ludlow *et al.*, 1985). Higher OA (Table 3) in hyb MSH-11 (0.8 MPa) than hyb ECH-86 (0.6 MPa) may also help in maintaining higher P_N rate under stress. In plants, higher g_s increases CO_2 diffusion into leaf thereby favouring higher P_N. Higher P_N could in turn favour a higher biomass and higher crop yields (Ashraf *et al.*, 2001). Although there was a decrease in g_s under stress, the results for P_N and g_s presented here for hybs and parents did not show a significant relationship (fig. 1a and 1b). Winter *et al.*, (1988) considered that g_s was not a good selection criterion for drought resistance.

The higher WUE in hyb. MSH-11 than parents indicated heterosis for WUE in this hyb. The higher WUE in this hyb (2.5μ mol CO_2/ mol H_2O) as compared to hyb ECH–86 (2.0μ mol CO_2/mol H_2O) may be due to the higher P_N rate in hyb MSH-11 under stress. The less reduction in P_N rate during water stress in hyb MSH-11 may thus contribute for better plant growth and better yield response to drought in this hyb. Ashraf *et al.*, (2001) reported strong association of plant growth with P_N in okra cultivars and not with g_s and WUE under drought. The hybs have been found to have a complementary relationship between source and sinks which leads to yield heterosis (Sinha and Khanna 1975).

The results indicate that hyb MSH-11 of hot pepper performed better as compared to the hyb ECH-86 and shown the heterosis for certain physiological parameters like P_N, WUE and TDM in hybrid MSH-11 under stress. The expression of heterosis of physiological parameters in the hyb MSH-11 may be a contributing factor for better performance of this hyb under stress, though further study is needed to establish relationship between heterosis of these parameters and plant tolerance under water stress in hot pepper.

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