



Osmotic adjustment, drought tolerance and yield in castor (*Ricinus communis* L.) hybrids

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ABSTRACT

A study was conducted to analyse the association of osmotic adjustment (OA) with drought tolerance and yield in castor (*Ricinus communis* L.). Hybrids (GCH4, DCH32 and DCH177) and their respective parents (VP-1, 48-1, LRES17, DCS5, DPC9 and DCS9) were assessed for their osmotic adjustment, leaf water relations, accumulation of compatible solutes in relation to seed yield in response to moisture stress at primary spike development stage. OA increased with increasing stress period up to 33 days and the increase was more rapid in the high OA (HOA) genotypes. HOA genotypes also had higher leaf RWC and ELWRC and maintained higher leaf water potentials (Ψ_1) compared to LOA genotypes under water deficit. Genotypes with HOA accumulated greater levels of proline, total soluble sugars (TSS), total free amino acids (FAA) and potassium than those with LOA in response to water deficit. Contribution of TSS was the maximum (61%), compared to FAA (17%), proline (12%) and potassium (2.8%) to the Ψ_s at 33 days after imposing water deficit indicating that sugars were the major contributors towards OA in castor leaves. A positive relationship existed between OA of expanded leaf 33 days after imposing stress ($r=0.8539$) and total seed yield under water-limited conditions in various castor genotypes tested and HOA genotypes had higher total seed yield than genotypes with LOA. Genotype variability exists for OA and it is a heritable trait in castor. Hybrids followed their superior parents in terms of OA. HOA genotypes of castor produced significantly higher seed yield than LOA genotypes. Accumulation of TSS contributed largely to the OA in castor.

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1. Introduction

Osmotic adjustment (OA), the active accumulation of solutes in response to drought has been reported to be an important drought adaptation mechanism in several crop plants (Hare et al., 1998; Moinuddin and Khanna-Chopra, 2004; Ashraf and Foolad, 2007; Martínez et al., 2005; Yousifi et al., 2010). OA leads to maintenance of turgor, through better extraction of water from the soil, stimulates root growth (Ali et al., 1999; Maggio et al., 2005; Kusaka et al., 2005; Gonzalez et al., 2010) and facilitates better remobilization of pre-anthesis assimilation to the developing seed (Morgan, 1980; Subbarao et al., 2000). A positive association of OA with grain yield under water-limited environments has been demonstrated in sorghum (Tangpremsri et al., 1995), wheat (Morgan and Condon, 1986; Blum et al., 1999; Morgan, 2000; Moinuddin et al., 2005; Zivack et al., 2009) barley (Blum, 1989; Gonzalez et al., 2009), chickpea (Morgan et al., 1991; Moinuddin and Khanna-Chopra, 2004) and pigeon pea (Subbarao et al., 2000). Similarly greater seed yield

of genotypes with higher OA (HOA) than those with lower OA (LOA) has also been reported in various crops (Ludlow et al., 1990; Morgan et al., 1991; Moinuddin and Khanna-Chopra, 2004), although OA in general is regarded only as an adaptive mechanism under drought. Never the less, there are also a few reports suggesting negative (Grumet et al., 1987; Kirkham, 1988) or no relationship (Shackel and Hall, 1983; Tangpremsri et al., 1995) between OA and seed yield under stress conditions.

Castor (*Ricinus communis* L.) is one of the major commercial non-edible oilseed crops grown in semi-arid and arid regions of India, China and Russia and is reported to be drought tolerant. Castor oil normally contains a high concentration of ricinoleic acid, over 85%, which confers distinctive industrial properties to the oil (Velasco et al., 2005). Such properties are of great value for a number application in many industrial fields, such as paints and varnishes, nylon-type synthetic polymers, hydraulic fluids and lubricants, and cosmetics (Ogunniyi, 2006). Because of its multifarious industrial applications, castor oil enjoys tremendous demand world-wide, estimated at about 220,000 tons per annum of which only 60 percent can be met with the current production estimates worldwide. One of the strategies to overcome demand and supply gap would be to evolve high yielding drought tolerant varieties for taking up

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Table 1
Physical and chemical characteristics of the soil used in the experiment.

Texture	Sandy loam
Sand (%)	59.3
Silt (%)	14.9
Clay (%)	16.8
pH	7.9
Electrical conductivity (m mhos cm ⁻¹)	0.20
Organic carbon (%)	0.35
Total nitrogen (%)	192.4
Available phosphorus (kg ha ⁻¹)	28.7

large scale planting waste and marginal lands in the arid and semi-arid tropics. Apart from various genetic improvement studies in germplasm to evolve varieties with high oil content (Murphy, 1992; Woodend, 1993) few studies have focussed on the mechanism of drought tolerance especially on the osmotic adjustment and accumulation of various compatible solutes in castor as a possible step for evolving drought tolerant hybrids or varieties. In view of the above facts, the present investigation was an attempt to assess the association of osmotic adjustment (OA) with drought tolerance and yield in three hybrids of castor and their respective parents.

2. Materials and methods

A field experiment was conducted during the post-rainy season (November to May) of 2001–2002. Soil physical and chemical properties and weather during the season are presented in Table 1 and Fig. 1 respectively. There were three replications and the experimental design was split plot with moisture status as the main plot and genotype as sub-plot. The two main plots represented (a) adequately irrigated condition (T_1), wherein irrigation was given to the crop based on its requirement according to the agronomic recommendations or (b) moisture stress at primary spike development stage (T_2), wherein irrigation was completely withheld to the crop for a period of about 50 days (between 70 and 120 days after sowing). The end of stress was determined by the day on which the genotypes reached water potentials of about -2.25 MPa.

Three hybrids and their respective parents were used as for the experiment the details of which are: Hybrid GCH 4 from Female Parent VP-1 and Male Parent 48-1; Hybrid DCH 32 from Female Parent LRES 17 and Male Parent DCS-5 and Hybrid DCH 177 from Female Parent DPC-9 and Male Parent DCS-9.

Four samplings were taken up during the moisture stress period coinciding with 11, 22, 33, and 45 days after imposing moisture stress and last sampling one week after relieving stress. Youngest fully expanded leaf (second leaf from the top) was used for esti-

mation of relative water content (Barrs and Weatherley, 1962), leaf water retention curves, solute potential (Vapour pressure Osmometer-Model 5500 Wescor Inc., Logan UT, USA) and leaf water potentials (Soil Moisture Equipments Corp., Santa Barbera, USA) according to Scholander et al. (1966).

Osmotic adjustment was calculated from the measured values of solute potential and relative water content (Babu et al., 1999). The OP_{100} was calculated as:

$$OP_{100} = OP \left[\frac{(RWC - B)}{(100 - B)} \right]$$

where RWC is relative water content and B is apoplastic water. A constant B -value of 20 per cent was used for both stressed and non-stressed leaves of all cultivars, since B did not change with cultivar or dehydration (Turner et al., 1986).

Proline (Bates et al., 1973), total sugars (Dubois et al., 1956), potassium (Chapman and Pratt, 1961) and amino acids (Moore and Stein, 1948) contents were estimated from the cell sap. The ψ_s of each solute was estimated by van't Hoff equation and expressed as percentage of the total measured ψ_s to assess their relative contribution. Seed yield was recorded and the data were subjected for ANOVA (Gomez and Gomez, 1984).

3. Results

3.1. Water relations and osmotic adjustment

Withholding water led to a progressive decrease in relative water content (RWC), leaf water potential (ψ_L) and solute potential (ψ_s) in all the castor genotypes (Fig. 2). Genotypes with higher OA had 1.4-fold higher ψ_L than those with low OA. Similarly genotypes with higher OA also retained higher RWC compared to those with low OA (LOA). Under moisture stress, hybrids had 4.6 per cent higher RWC than the parents. Hybrids had also showed a higher reduction (50%) in ψ_s under stress compared to the parents (44.5%).

The decline in ψ_s was in general concomitant to the decline in ψ_L . The magnitude of decline in ψ_s with falling ψ_L and RWC was remarkably higher (Fig. 2) in genotypes, which showed higher OA (67%) than in those with no OA (8.2%). However, in genotypes with relatively LOA, ψ_s decreased but not as rapidly as ψ_L resulting in loss of turgor.

3.2. Osmotic adjustment (OA) capacity

The range of OA showed by castor genotype in this study was between 0.04 and 0.62 MPa (Fig. 3). GCH-4, 48-1, LRES-17, DCH-177

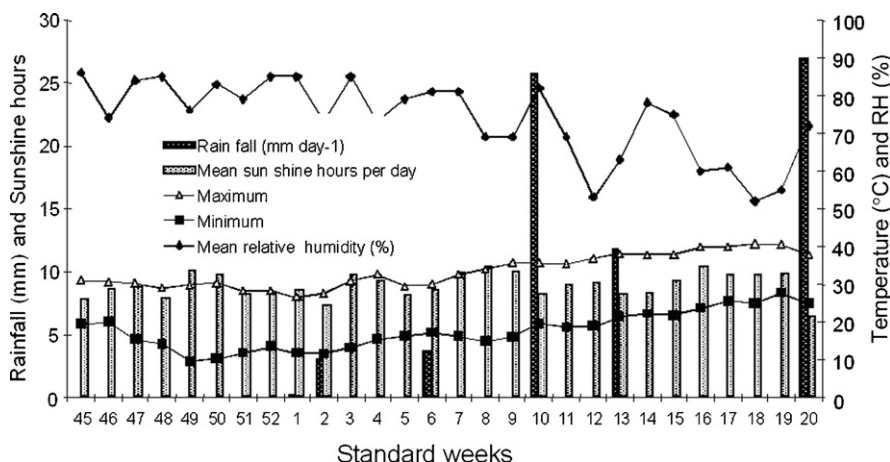


Fig. 1. Weekly meteorological data during crop season, depicting the maximum, minimum temperatures, rainfall, mean sunshine hours, and mean relative humidity.

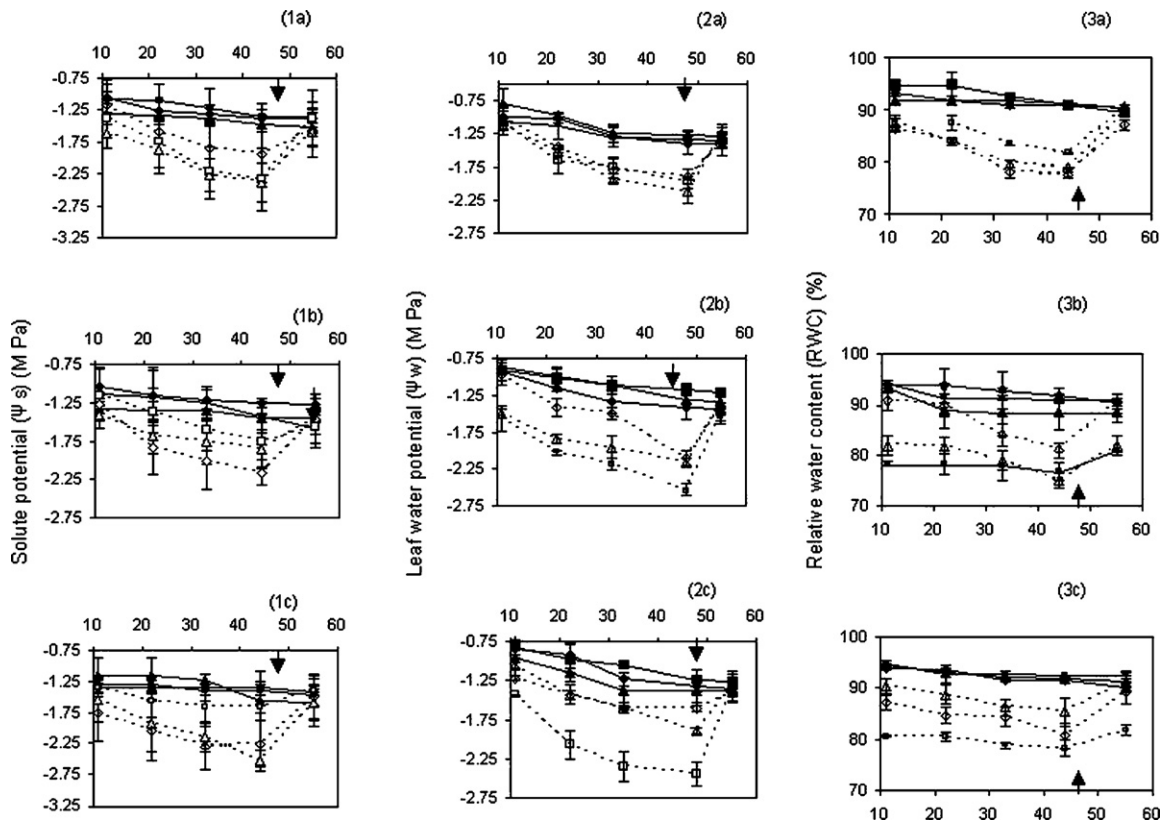


Fig. 2. Effect of water deficit (solid lines: control and dotted lines: stressed) and its relief (solid arrow) on solute potential (1), leaf water potential (2) and relative water content (3) in castor genotypes in hybrid (triangles) and parents (a) GCH-4, (b) DCH 32 and (c) DCH 177 male and female parents are represented by squares and circles respectively.

and DPC-9 showed high OA (0.43–0.82 MPa) while VP-1, DCH-32, DCS-5 and DCS-9 showed low OA (–0.02 to 0.17). The OA capacity of the genotypes, in particular that of the HOA, increased with the increase in moisture stress until 33 days after withholding water ($\sim \Delta \psi_1 = 0.5$ MPa). The increase in OA was more rapid in the genotypes, which had a higher capacity to adjust osmotically (Fig. 3).

3.3. Excised leaf water retention capacity (ELWRC)

Large differences were observed among castor genotypes in water holding capacity of excised leaves in the present study (Fig. 4). HOA genotypes DCH 177 and DPC 9 also retained more water than all the other genotypes. On the other hand, DCS 9 and DCS 5, which did not show any osmotic adjustment, also had very low ELWRC.

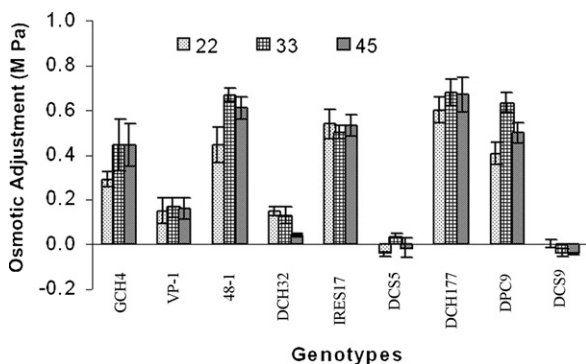


Fig. 3. Osmotic adjustment in various genotypes of castor at 22, 33 and 45 days after imposing water deficit respectively.

3.4. Accumulation of metabolites

Analysis of water stress related metabolites in leaves of castor genotypes revealed that major differences existed in the accumulation of total soluble sugars (TSS), total free amino acids (FAA), proline and potassium. Proline content was found to increase by more than 2-fold in T_2 between 7 and 33 days after imposition of stress compared to irrigated control (Table 2). HOA genotypes exhibited higher proline accumulation than those with LOA by the end of the stress period. On the seventh day of re-watering, proline accumulation decreased but was still higher than that of the irrigated control (Table 3).

Maximum build-up of TSS was observed only up to 33 days after imposing stress. TSS accumulated to the extent of 216.6 per cent at

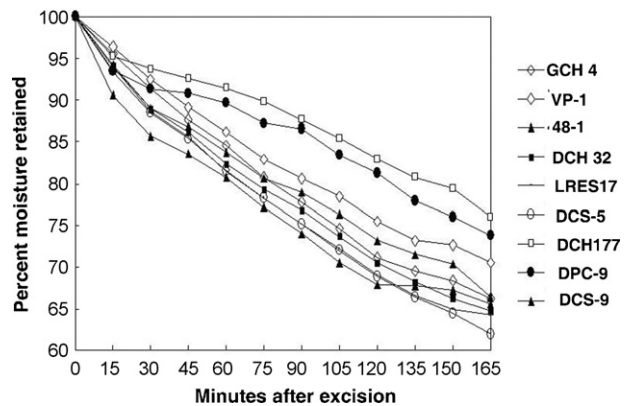


Fig. 4. Excised leaf water retention in castor genotypes differing in osmotic adjustment.

Table 2
Accumulation of proline, free amino acid (FAA), total soluble sugars (TSS) and potassium in leaves of castor genotypes 33 days after imposing moisture stress imposed at primary spike development stage moisture stress (post-rainy season, 2001).

Genotypes	Proline		FAA		TSS		Potassium	
	T ₁	T ₂	T ₁	T ₂	T ₁	T ₂	T ₁	T ₂
(mg g ⁻¹ dry weight)								
GCH-4	4.04	21.78	9.81	38.45	101.01	281.11	7.7	10.8
VP-1	4.63	28.84	10.96	44.34	87.69	148.46	6.0	8.4
48-1	4.27	29.26	9.85	44.61	80.27	301.52	6.2	9.8
DCH-32	3.70	22.38	9.76	38.01	97.09	129.91	6.6	8.5
LRES-17	3.37	32.33	9.80	48.56	81.10	217.34	7.8	11.4
DCS-5	4.02	15.27	9.99	32.01	91.20	156.27	5.8	7.4
DCH-177	3.61	32.24	8.86	48.41	72.87	291.73	6.1	10.4
DPC-9	3.41	32.49	9.75	47.78	92.09	262.35	6.5	9.6
DCS-9	4.17	18.68	10.88	35.30	83.86	156.71	5.9	7.8
Mean	3.91	25.93	9.96	41.94	87.46	216.16	6.5	9.3
CD at 0.05 P:T	0.51		0.98		5.16		0.43	
G	0.46		1.20		4.63		0.50	
T × G	0.65		1.72		6.55		0.71	
G × T	0.85		1.56		8.33		0.69	

Table 3
Accumulation of proline, free amino acid (FAA), total soluble sugars (TSS) and potassium in leaves of castor genotypes 7 days after recovery from moisture stress imposed at primary spike development stage moisture stress (post-rainy season, 2001).

Genotypes	Proline		FAA		TSS		Potassium	
	T ₁	T ₂	T ₁	T ₂	T ₁	T ₂	T ₁	T ₂
(mg g ⁻¹ dry weight)								
GCH-4	4.96	11.82	11.13	22.96	112.35	142.35	6.3	6.4
VP-1	5.29	10.60	11.11	20.74	97.17	149.29	5.7	4.2
48-1	5.08	10.96	11.10	22.70	85.96	146.27	5.0	5.3
DCH-32	4.69	9.09	10.91	20.78	111.30	145.46	5.4	5.4
LRES-17	4.18	13.99	8.97	24.78	95.14	150.04	6.3	6.8
DCS-5	4.52	5.58	10.27	20.22	102.22	150.98	3.9	3.7
DCH-177	4.45	12.93	11.10	23.72	82.05	146.69	5.6	6.0
DPC-9	4.52	14.51	10.97	24.68	99.00	141.04	5.8	6.2
DCS-9	5.21	8.08	10.59	18.96	94.55	152.62	4.1	3.8
Mean	4.77	10.84	10.68	22.17	97.75	147.19	5.3	5.3
CD at 0.05 P:T	0.09		3.45		1.48		NS	
G	0.22		3.86		3.68		0.49	
T × G	0.23		5.41		3.79		0.69	
G × T	0.15		5.41		2.45		0.93	

33 days after imposing stress (Table 2). HOA genotypes had 2.8–fold greater TSS than those with LOA at 33 days after imposing stress. Tolerant genotypes 48-1 and DCH 177 accumulated 2-fold more TSS than susceptible genotypes DCS 5 and DCS 9. At one week after re-watering, TSS accumulation under stress treatment was still 50.6 per cent higher than that of the control.

FAA accumulated under stress in all the genotypes. Stressed leaves had 30 per cent higher FAA accumulation than that of the control (Table 2).

In response to moisture stress, potassium accumulated to a lower extent compared to proline, sugars and amino acids in the leaves of castor genotypes (Table 2). At 33 days after imposing moisture stress, HOA genotypes had 1.2-fold greater accumulation of K⁺ than LOA genotypes. When recovery was assessed one week after re-watering, the levels under stress were almost equal to those of the control plants (Table 3).

3.5. Relative contribution of various compatible solutes towards OA

The compatible solutes, viz TSS, FAA, proline and potassium could account for 81–98 per cent of the Ψ_s in water stressed leaves. The extent of contribution towards Ψ_s was 61%, 17%, 12% and 2.8% by TSS, FAA, proline and potassium respectively at 33 days after imposing water deficit (Fig. 5).

3.6. Association of OA and seed yield

A positive relationship was observed between OA of expanded leaf 33 days after imposing stress ($r=0.8539$) and total seed yield under water-limited conditions in various castor genotypes tested (Fig. 6).

4. Discussion

4.1. Osmotic adjustment and leaf water retention

Genotypes which had higher OA such as DCH 177 and 48-1 were also able to maintain consistently higher ψ_1 , which facilitated maintenance of turgor under stress. On the other hand DCS 5 and DCS 9, which showed no OA, had much lower leaf water potential. The decline in ψ_s was in general concomitant to the decline in ψ_1 indicating that the leaf turgor was maintained largely. These observations are consistent with the view that capacity to develop more negative ψ_s through accumulation of solutes is associated with mitigation of deleterious effects of moisture stress (Turner and Jones, 1981; Morgan, 1984, 1995; Moinuddin and Khanna-Chopra, 2004; Gonzalez et al., 2008).

Increase in OA in response to progressive water deficits is known to occur due to active accumulation of solutes (Morgan, 1984). However, higher OA with increasing water deficits particularly at

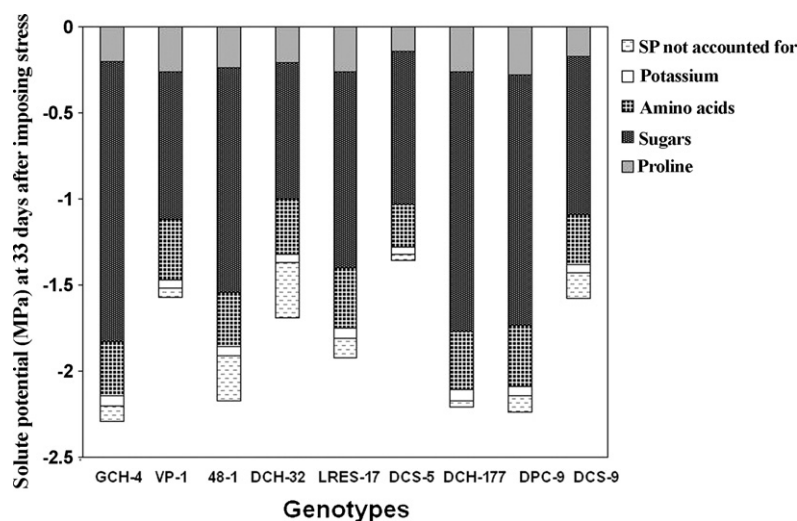


Fig. 5. Relative contribution of various compatible solutes towards solute potential at 33 DAS.

later stages of ontogeny has been attributed to passive accumulation of solutes. In this study, the OA declined slightly beyond 33 days after imposing stress. Hybrids had higher OA (1.7–2-folds) than the parents. This study also confirms the results of other workers regarding substantial phenotypic variability of OA (Morgan, 1995; Blum et al., 1999). The wide range of variability among the genotypes also indicates the suitability of OA as selection criterion in castor under water deficit environments.

The HOA genotypes also had higher ELWRC (Fig. 4) indicating that this trait appears to be useful screening criterion for drought tolerance in castor. Maintenance of high OA seems to have enabled the excised leaves to retain moisture for longer periods in this study. A positive association of ELWRC with OA is expected as the role of OA in maintaining turgor and plant growth under water deficit had been established in several crops (Morgan and Condon, 1986; Morgan, 1995; Grammatikopoulous, 1999; Khanna-Chopra et al., 1994; Moinuddin and Khanna-Chopra, 2004; Moinuddin et al., 2005). Also genotypic differences in ELWRC were shown to be correlated with drought tolerance (Sarkar et al., 1991).

4.2. Genotypic differences in accumulation of compatible solutes and yield

During osmotic adjustment, the cells tend to accumulate and sequester compatible organic solutes in order to maintain the

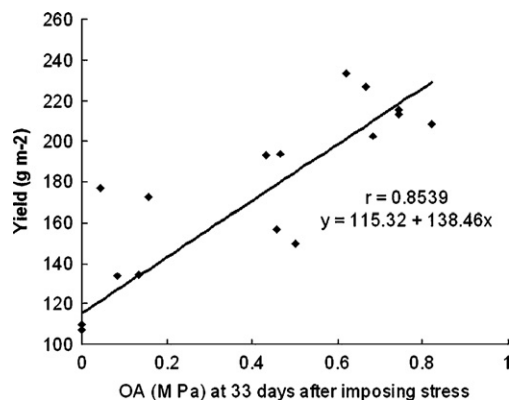


Fig. 6. Relationship of osmotic adjustment with seed yield in castor genotypes.

solute potential and osmotic equilibrium (Hare et al., 1998; Zhang et al., 1999). Several ions, amino acids, quaternary amines, sugars and polyols accumulate during osmotic adjustment although their presence, amount and distribution within the cells vary widely among crop species and cultivars (Hare et al., 1998; Zhang et al., 1999; Larher et al., 2009; Zhou and Yu, 2010).

Proline and FAA increased up to the end of the stress period, while TSS increased only up to 33 days after imposing stress, when the maximum OA was observed. Genotypic differences in proline accumulation during drought stress have been reported in various crops, and it is generally accepted now that proline may play a more complex role in conferring drought tolerance than simply contributing to OA (Blum and Ebercon, 1976; Zhang et al., 1999; Kavi Kishor et al., 2005).

Maintenance of higher osmotic potential (4.1%) under moisture stress compared to irrigated control even at one week after re-watering could be related to this accumulation. Accumulation of more sugars might result in cell membrane stability by replacing the water molecules from the hydrated cells, and are suspected to promote vitrification at ambient temperatures and hence protect membranes and permit a stable quiescent state (Crowe et al., 1998). Accumulation of amino acids at lower leaf water potentials was earlier reported in Sesamum (Vyas et al., 1983). HOA genotypes accumulated 20.6 per cent higher FAA content than that of LOA genotypes.

Ion accumulation in water stress tissue can occur only till ion uptake processes are not influenced by drought stress. TSS, which contributed more to OA, also decreased rapidly compared to proline and FAA upon re-watering. The accumulation of proline here can be said to indicate a drought response and its decline on re-watering confirms that. On the other hand it should be noted that a response to drought stimuli could also have the function of triggering a countering action harmful effects of the stimuli, which in this case is drought. The differences in proline accumulation observed in LOA and HOA under control and stressed plants further supports the mechanistic theory that proline accumulation may be an integral component of plants adaptation to water stress.

The TSS was the major contributor towards OA in castor leaves unlike in case of wheat wherein potassium was found to be the major osmolyte (Morgan, 1992). The HOA genotypes, hybrid GCH 4 and DCH 177 accumulated relatively higher TSS, potassium, lower proline and FAA over its better parents, respectively under stress. On the other hand, LOA genotype DCH 32 showed relatively lower accumulation of TSS as well as potassium and relatively higher lev-

els of proline and FAA under stress over its parents. The similarity in the trends observed in OA and in the accumulation of TSS among the hybrids and parents also indirectly indicates that TSS contributed maximum to OA, in the castor genotypes tested. These results are in agreement with those obtained for sorghum by (Ludlow and Muchow, 1990; Santamaria et al., 1990) and for wheat (Morgan, 1995; Babu et al., 1999), pea (Rodríguez-Maribona et al., 1992) and chickpea (Moinuddin and Khanna-Chopra, 2004).

Genotypes with relatively HOA had 53% higher total seed yield than genotypes with LOA. The differences in OA are conditioned by alternative alleles of OA gene at a single major locus (Morgan et al., 1991). Maintenance of leaf turgor in castor genotypes as evidenced by higher relative water content (1.1-fold) and leaf water potential (1.3-fold) might have resulted in continued metabolic activity during seed filling. This might have led to the maintenance of greater sink demand in HOA genotypes compared to those with LOA genotypes. Interestingly, in the study, genotypes with greater capacity of OA also produced higher seed yield. Improvement in yield due to OA has been reported (Morgan, 1995; Chimenti et al., 2002; Moinuddin and Khanna-Chopra, 2004; Moinuddin et al., 2005). To the best of our knowledge this is the first report on the association of OA with yield in castor.

In summary, the results demonstrated that genotype variability exists for OA. Hybrids followed their superior parents in terms of OA. HOA genotypes of castor produced significantly higher seed yield than LOA genotypes. Accumulation of TSS contributed largely to the OA in castor in contrast to the fact that K has been found to contribute to OA in most crops.

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