The Influence of Water and Gas Exchange Parameters on Grafted Grapevines Under Conditions of Moisture Stress

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Among the four grape varieties that were subjected to moisture stress, Flame Seedless and Thompson Seedless recorded the highest relative water content, osmotic potential and water potential compared to Sharad Seedless and Tas-A-Ganesh. Similarly, Flame Seedless and Thompson Seedless recorded the maximum rate of photosynthesis, the minimum transpiration rate, and thus increased water-use efficiency. Sharad Seedless on its own root had the lowest water-use efficiency. Budding the respective four varieties on different rootstocks and subjecting them to moisture stress resulted in significant differences in various physiological parameters that influence water-use efficiency. When Sharad Seedless was budded on Dog Ridge rootstock and subjected to moisture stress, it resulted in increased water potential, osmotic potential and water use efficiency compared to other rootstocks. This suggests that rootstocks have an influence on the physiological mechanisms of scion leaves. Hence, the genotypic selection of rootstocks for establishing vineyards under drought conditions is of great importance.

In the past, in Indian viticulture, all commercial varieties of grapes were grown on their own roots, as most of the soils were free from soil-borne problems like nematodes, phylloxera and salts. However, nowadays, with the increasing levels of soluble salts in the soil and ground water, and also due to over-exploitation of aquifers, drought and salinity are major constraints in semi-arid regions, where most of the grape growing areas of India are concentrated. Worldwide, rootstocks are now playing a major role in combating the abiotic stresses like drought and salinity in the major grape-growing regions of the world.

Among the several adoptive strategies applied to drought tolerance, improving the efficiency of water use for biomass production is perhaps the most relevant mechanism. (Lincoln & Eduardo, 2002). Water use efficiency (WUE) can be defined as biomass produced over a period of time to total water transpired during the same period of time. WUE is also referred to as the transpiration efficiency. At the single-leaf level, WUE is the ratio of the number of moles of carbon assimilated to the number of moles of water transpired. According to the yield model of Passioura (1986), WUE is an important determinant of the total biomass production. Despite the realization of the importance of WUE in crop improvement, rapid progress in improving this feature was not achieved. This could be attributed to the lack of a suitable technique for the rapid screening of genetic variability in WUE.

The rooting behaviour of the rootstocks has an obvious effect on the water relations of scion leaves. In this context, basic research work has revealed that photosynthesis and stomatal conductance, which are the main physiological parameters in drought tolerance, are affected by the rootstocks used and its effect is also scion specific (Sobhana, 1988). Since grafting/budding provide new root systems to the scion varieties, it is important to understand whether rootstocks have some effect on the scion leaves after grafting.

Hence the present investigation was carried out to study the effect of some rootstocks on the physiological response of some major commercial grape varieties grown in India.

MATERIALS AND METHODS

Experimental layout

This experiment was conducted in two parts at the experimental farm of the Indian Institute of Horticultural Research, Bangalore, India, during 2002-03 and 2003-04, under open conditions. The experimental site is situated at 14°N latitude and 77°E latitude. It is in an elevated plain at an altitude of 863 m above the mean sea level. The climate is mild and slightly humid. The maximum and minimum temperatures were 30-34.5°C and 18-21°C respectively; the relative humidity was 65-70% in the morning (08:00) and 30-35 % during the afternoon (13:00), while the evaporation rate ranged from 6.25 to 8.3 mm during the experimental period.

In the first part of the experiment, during September 2002, rooted cuttings of the following grape varieties: Flame Seedless, Thompson Seedless, Sharad Seedless (syn: Kishmish Cherney) and Tas-A-Ganesh (mutant of Thompson Seedless, popular in Maharashtra state), were transplanted to 14” earthen pots (20-kg capacity) containing a potting mixture of red earth, sand and FYM, in the ratio 2:1:1. The water-holding capacity of the potting mixture was 30%. When the plants had attained the age of six months (April 2003), they were subjected to two levels of moisture stress, viz. 50% stress and 100% stress, over a period of 14 days. A control experiment with no stress, viz.100% irrigation, was also carried out. The plants were manually irrigated, with the

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following volumes of water: 1.5 liters for the control treatment (no stress), about 0.75 liters for the 50% stress experiment and no irrigation for the 100% stress treatment. The experiment was designed in a factorial randomized design with three replications consisting of two factors, viz. irrigation levels and grape varieties. Each replication consisted of 10 vines.

The following gas exchange parameters were recorded on three fully matured leaves per vine: photosynthesis rate (μ mole/m^2/sec), transpiration rate (m mole/m^2/sec) and stomatal conductance (μ mole/m^2/sec), using a portable photosynthesis system (Model LCA_3, ADC, Hudgesdon, England). All the observations were recorded between 09:00 and 11:00. The area of the leaf chamber was 6.25 cm^2 and the time required for each reading was 30 seconds. Water use efficiency at single-leaf level was derived using values for the photosynthesis rate and transpiration rate.

Leaf samples (three matured leaves per vine, usually the 5th leaf from the tip of the shoot) were collected from the experimental plants in the morning hours after recording gas exchange parameters and then brought to the laboratory in an icebox. The leaves were deep-frozen for between 8 and 10 hours and later thawed. The sap was extracted by squeezing manually and then used for measuring the water potential and osmotic potential. The leaf sap was kept in the sample chamber. Leaf water potential was measured using a water potential system CR 7, Campbell Scientific Inc., USA. The time required to record the readings was five minutes. The leaf osmotic potential was measured using a vapour pressure osmometer 5100 C Wescor. The time taken to record one observation was 80 seconds. The osmotic potential values were expressed in MPa. The relative water content (RWC) was measured as per the procedures of Barrs and Weatherly (1962).

In the second part of the experiment, based on the WUE values of the above-mentioned four varieties at 50% stress, on day 14 three varieties having the highest WUE, namely Flame Seedless, Thompson Seedless and Sharad Seedless, were selected in order to study their performance when they were budded on the three rootstocks Dog ridge, Salt Creek, and *Vitis Champinii* clone (popularly known as VC clone). The nine stionic combinations were: Flame Seedless on Dog ridge, Salt Creek and VC clone, Thompson Seedless on Dog ridge, Salt Creek and VC clone, Sharad Seedless on Dog Ridge, and Salt Creek and VC clone. The experiment was laid out as a factorial randomized design with two factors, *viz*, grape varieties and rootstocks, to determine the interaction of rootstocks and varieties after budding, at different levels of irrigation.

Chip budding was done during September 2003 on one-year-old rootstocks grown in 14” earthen pots filled with standard potting mixture (as mentioned above). When the budded plants attained six months age (April 2004), they were exposed to two levels of stress, namely 100% stress and 50%, for 14 days. Again, a control experiment with no stress, viz.100% irrigation, was also carried out. The budded plants under 100% stress could not survive beyond 3 to 4 days. Hence observations were recorded in only two cases: treatment of control and 50% stress. On day 14, i.e. at the time of termination of the stress treatments, gas exchange parameters, leaf water potential and leaf osmotic potential were measured as explained above.

Statistical analysis

The statistical analysis was carried out as per the procedures of Gomez and Gomez (1984). The comparison of treatments was carried out using standard error of mean and critical difference at $p < 0.05$.

RESULTS AND DISCUSSION

Relative water content, water potential and osmotic potential

It is evident from Table 1 that no variety survived until day 14 of the stress cycle at 100% stress treatment. Hence observations were recorded only for the treatments at 50% stress, and for the control (no stress). When the ungrafted varieties were subjected to different levels of moisture stress, Tas-A-Ganesh recorded the lowest RWC at 50% moisture stress on day 14 of the stress cycle, followed by Sharad Seedless. The highest (less negative) osmotic potential was recorded for Flame Seedless at 50% moisture stress; it was -1.38 MPa (see Table 1). The lowest osmotic potential was recorded in Tas-A-Ganesh, followed by Sharad Seedless.

When the same varieties were budded on rootstocks and subjected to moisture stress it was found that rootstocks had a significant

TABLE 1

Influence of moisture stress on relative water content (RWC %), water potential and osmotic potential in grape varieties on 14th day of stress cycle.

Varieties (V)	**RWC (%)**			**Water potential (-MPa)**			**Osmotic potential (-MPa)**		
	S 1	**S 2**	**S 3**	**S 1**	**S 2**	**S 3**	**S 1**	**S 2**	**S 3**
Flame Seedless	87.36	71.94	*	1.15	1.31	*	1.48	1.38	*
Thompson Seedless	87.39	71.17	*	1.21	1.48	*	1.76	1.48	*
Sharad Seedless	81.98	67.04	*	1.28	1.51	*	1.38	1.81	*
Tas-A-Ganesh	80.25	61.64	*	1.23	1.64	*	1.25	1.90	*
	V	**S**	**V ×S**	**V**	**S**	**V ×S**	**V**	**S**	**V ×S**
P < 0.005	5.041	3.564	NS	NS	NS	NS	0.218	0.514	NS

S: Stress levels
S 1: control (100% irrigation); **S 2**: 50% stress (50% irrigation); **S 3**: 100% stress (no irrigation)
*: Plants were wilted and hence observations not recorded.
NS: Not significant

influence on the RWC of budded varieties, both in the control and in the 50% stress experiments. The RWC was lower in all the varieties, on all the rootstocks, at 50% stress compared with when under control conditions. Flame Seedless on Dog Ridge had maximum RWC values of 81.94% at 50% stress, followed by Sharad Seedless on Salt Creek. The lowest RWC was recorded in Thompson Seedless and Flame Seedless on the VC clone. The rate of increase in RWC in Sharad Seedless budded on Dog Ridge, compared with ungrafted Sharad Seedless, indicated that rootstocks influence the water content of sensitive varieties under moisture stress conditions. There was a decrease in water potential of budded vines at 50% stress compared with when under control conditions. Flame Seedless on Dog Ridge had the highest water potential (less negative) at 50% stress followed by Flame Seedless on Salt creek. The lowest water potential of -1.64 MPa was recorded in Thompson Seedless budded on the VC clone. Sharad Seedless exhibited maximum water potential when budded on Dog Ridge and subjected to 50% moisture stress compared with when it was budded on Salt Creek and VC clone. Similarly, Flame Seedless and Sharad Seedless budded on Dog Ridge had the highest osmotic potentials of -1.33 MPa and -1.40 MPa respectively, while it was the lowest in Thompson Seedless on Dog Ridge and VC clone rootstocks. Osmotic adjustment was lowest in Thompson Seedless on the rootstocks Dog Ridge and VC clone (see Table 2).

Among the varieties on their own roots, and after budding on different rootstocks, Flame Seedless was able to maintain a high RWC in leaves at 50% stress when budded on Dog Ridge compared with when budded on Salt Creek and VC clone. Similarly, Flame Seedless and Sharad Seedless on Dog Ridge had the highest water potential compared with when budded on Salt Creek and VC clone. The increase in water potential in Flame Seedless and Sharad Seedless on Dog Ridge was coupled with a decreased osmotic potential. This indicated a better osmotic adjustment. Sharad Seedless on its own root had a lower osmotic potential of -1.81 MPa at 50% stress, and this increased to -1.40 MPa when budded on Dog Ridge. Similarly, the potassium (K) content in Flame Seedless and Sharad Seedless increased significantly on Dog Ridge compared with on their own roots (data not shown). As K is an important inorganic osmolyte under water-stress conditions, this might be the reason for the higher water potential observed under stressed conditions. Rootstock 101-14 reduced the water potential of Niagara Rosada compared with when it was grafted on 1103 P. However, little difference in RWC was observed among irrigation levels/rootstock scion combinations (Souza *et al.*, 2001). Similarly, the Italia variety of grape grafted on St. George rootstock had the lowest water potential compared with when grafted onto SO-4 and 99R.

Water stress can reduce both water and turgor potential by osmotic adjustment (Nagarajah, 1989). In the present investigation, under the 50% moisture stress conditions, the rootstock Dog Ridge must have influenced the Flame Seedless and Sharad Seedless to maintain turgor and water relations with increased

TABLE 2

Influence of soil moisture stress on water relations in budded vines on 14th day of stress cycle.

Rootstock / Scion	Control (100% irrigation)			50% stress (50% irrigation)		
	Dog Ridge	Salt Creek	V.C. clone	Dog Ridge	Salt Creek	V.C. clone
Relative water content (%)						
Flame Seedless	88.47	86.20	79.13	81.94	76.20	65.17
Thompson Seedless	88.40	88.65	83.78	77.86	78.53	64.64
Sharad Seedless	88.37	86.90	83.91	76.30	79.62	66.49
	Rootstock	**Scion**	**Interaction**	**Rootstock**	**Scion**	**Interaction**
P < 0.005	3.02	NS	NS	3.95	NS	NS
Leaf water potential (-MPa)						
Flame Seedless	0.95	1.15	1.19	1.17	1.39	1.51
Thompson Seedless	1.17	1.05	1.23	1.53	1.40	1.64
Sharad Seedless	1.03	1.00	1.04	1.44	1.55	1.51
	Rootstock	**Scion**	**Interaction**	**Rootstock**	**Scion**	**Interaction**
P < 0.005	NS	NS	NS	NS	NS	NS
Leaf osmotic potential (-MPa)						
Flame Seedless	1.22	1.20	1.27	1.33	1.34	1.49
Thompson Seedless	1.16	1.16	1.28	1.62	1.40	1.61
Sharad Seedless	1.12	1.10	1.12	1.40	1.42	1.55
	Rootstock	**Scion**	**Interaction**	**Rootstock**	**Scion**	**Interaction**
P < 0.005	0.017	0.017	0.030	0.062	0.062	NS

NS: Not significant

osmotic adjustment. Thompson Seedless maintained a higher osmotic potential on Salt Creek, to maintain turgidity.

There may be genetic differences among rootstocks and varieties that influence the water relations, as suggested by Zamboni & Iacono (1998). They recorded an osmotic potential range in the range of -0.8 MPa to -0.20 MPa in Sauvignon Blanc grafted on 3309 C, 775 P, *Vitis riparia*, *Vitis berlandieri* and *Vitis rupestris*. In their study, different rootstocks, under similar conditions, were found to accumulate different solutes in the scions.

Gas-exchange parameters

Flame Seedless and Thompson Seedless on their own roots recorded higher photosynthetic rates and decreased transpiration rates at 50% stress on day 14 of the stress cycle. Sharad Seedless and Tas-A-Ganesh recorded the lowest rate of photosynthesis and the highest transpiration rate at 50% stress on day 14 of the stress cycle. Significant differences were observed in stomatal conductance among varieties grown on their own roots. This was also due to interaction between varieties and irrigation levels on day 14 of the stress cycle. Flame Seedless and Thompson Seedless recorded the highest stomatal conductance at 50% stress on day 14 of the stress cycle, while it was lowest in Sharad Seedless and Tas-A-Ganesh (see Table 3).

It is evident from Table 4 that the rate of transpiration was not affected by rootstocks under control conditions. There was a decrease in the rate of transpiration at 50% stress in all the stionic combinations except Sharad Seedless on VC clone. Flame Seedless on Dog Ridge exhibited the lowest transpiration rate, followed by Sharad Seedless on Dog Ridge. All three varieties on VC clone rootstock transpired more than when either on Dog Ridge or on Salt Creek. Similarly, all the varieties budded on Dog Ridge and Salt Creek had a higher rate of photosynthesis, while the lowest was recorded for varieties budded on VC clone. Stomatal conductance under control conditions (100% irrigation) was not influenced either by rootstocks, scion varieties, or their interactions. This suggests that when plants are supplied with sufficient irrigation, the plants will not struggle much to improve their WUE by various physiological mechanisms. The need for exhibiting various physiological mechanisms to increase WUE arises only under water scarcity conditions. But here, at 50% stress, rootstocks and varieties had a significant influence on stomatal conductance. Flame Seedless had maximum stomatal conductance at 50% stress on VC clone, while Sharad Seedless and Thompson Seedless had highest stomatal conductance on Salt Creek. The least stomatal conductance was recorded in Flame Seedless on Dog Ridge followed by Sharad Seedless on Dog Ridge (see Table 4). Budding the varieties on Dog Ridge rootstock increased water-use efficiency of all the three varieties. The lowest WUE was recorded in Sharad Seedless budded on VC clone. But, on their own roots, Sharad Seedless and Tas-A-Ganesh recorded the lowest WUE on day 14 of the stress cycle at 50% stress, while the highest value was recorded in Flame Seedless, followed by Thompson Seedless (see Table 2).

The literature is not very clear about the relationship between the rate of photosynthesis in rootstocks on their own roots and the influence on scion varieties after budding. Some studies have shown the influence of rootstocks on the rate of photosynthesis of scion leaves, as reported by Brown *et al*, (1985), Sharma and Singh (1989) and Iacono *et al*, (1998), for a wide range of crop species like apple, citrus and grapes. In the present investigation there was a significant change in the rate of photosynthesis at 50% stress in all the rootstock/scion combinations. Further, there was a reduction in the rate of transpiration in all the rootstock/scion combinations. At 50% stress, initial WUE was influenced by the interaction of rootstocks and scions. Dog Ridge rootstock increased WUE of all the three varieties budded on it at 50% stress compared with in the control experiment. The decrease in transpiration rate might be due to decreased stomatal conductance at 50% stress, which is the major contributing factor to increased WUE under moisture stress. Rootstocks had significant influence on stomatal conductance of scions after budding and this suggested some possible signal from the rootstock which must have contributed to a reduction in stomatal conductance in response to soil perturbation. Bica *et al.* (2000) observed significant effects of rootstock on leaf area, chlorophyll content, stomatal conductance and quantum yield in Pinot Noir and Chardonnay. Chardonnay grafted on 1103 P showed a higher rate of photosynthesis, stomatal conductance and chlorophyll content than when grafted on

TABLE 3

Influence of moisture stress on gas exchange parameters in grape varieties on 14th day of stress cycle.

Varieties (V)	Rate of photosynthesis (µ mole/m²/sec)			Transpiration rate (m mole/m²/sec)			Stomatal conductance (µ mole/m²/sec)			Water use efficiency (µ mole/m mole)		
	S 1	**S 2**	**S 3**	**S 1**	**S 2**	**S 3**	**S 1**	**S 2**	**S 3**	**S 1**	**S 2**	**S 3**
Flame Seedless	10.0	9.10	*	10.50	6.90	*	0.57	0.41	*	0.96	1.33	*
Thompson Seedless	9.63	8.00	*	10.40	7.80	*	0.52	0.40	*	0.91	1.02	*
Sharad Seedless	7.50	7.06	*	10.33	8.90	*	0.42	0.39	*	0.72	0.78	*
Tas-A-Ganesh	7.83	5.73	*	10.76	9.50	*	0.43	0.36	*	0.72	0.60	*
	V	**S**	**V ×S**	**V**	**S**	**V ×S**	**V**	**S**	**V ×S**	**V**	**S**	**V ×S**
P < 0.005	1.080	1.380	NS	0.371	0.321	0.643	0.042	0.037	0.074	0.134	0.116	0.232

S: Stress levels
S 1: control (100% irrigation); **S 2**: 50% stress (50% irrigation); **S 3**: 100% stress (no irrigation)
*: Plants were wilted and hence observations not recorded.
NS: Not significant

TABLE 4

Influence of soil moisture stress on gas exchange parameters in budded vines on 14th day of stress cycle.

Rootstock / Scion	Control (100% irrigation)			50% stress (50% irrigation)		
	Dog Ridge	Salt Creek	V.C. clone	Dog Ridge	Salt Creek	V.C. clone
			Rate of photosynthesis (μ mole/m2/sec)			
Flame Seedless	6.80	7.86	7.63	6.80	7.46	6.46
Thompson Seedless	5.80	7.76	7.46	6.73	7.20	6.36
Sharad Seedless	6.86	8.00	6.46	7.16	7.36	5.93
	Rootstock	**Scion**	**Interaction**	**Rootstock**	**Scion**	**Interaction**
CD at 5%	NS	NS	NS	NS	NS	NS
			Transpiration rate (μ mole/m2/sec)			
Flame Seedless	7.86	8.46	9.23	6.30	6.86	9.00
Thompson Seedless	8.23	8.80	8.46	7.33	8.43	7.93
Sharad Seedless	8.83	9.09	8.90	6.53	7.63	8.96
	Rootstock	**Scion**	**Interaction**	**Rootstock**	**Scion**	**Interaction**
P < 0.005	NS	NS	NS	0.554	NS	0.960
			Stomatal conductance (μ mole/m2/sec)			
Flame Seedless	0.64	0.73	0.74	0.27	0.36	0.43
Thompson Seedless	0.53	0.56	0.58	0.38	0.47	0.45
Sharad Seedless	0.64	0.67	0.64	0.32	0.42	0.37
	Rootstock	**Scion**	**Interaction**	**Rootstock**	**Scion**	**Interaction**
P < 0.005	NS	NS	NS	0.060	0.060	NS
			Instantaneous WUE (μ mole/ m mole)			
Flame Seedless	0.85	0.92	0.82	1.09	1.09	0.71
Thompson Seedless	0.70	0.87	0.87	0.89	0.85	0.80
Sharad Seedless	0.76	0.87	0.73	1.09	0.96	0.66
	Rootstock	**Scion**	**Interaction**	**Rootstock**	**Scion**	**Interaction**
P < 0.005	NS	NS	NS	0.137	NS	NS

NS: Not significant

SO-4. The response of scions towards the rate of photosynthesis is scion specific, and it varies with the species. This was confirmed by Sharma and Singh (1989), who recorded the highest photosynthesis on own rooted *Citrus limon* compared with when grafted on vigorous rootstocks like *Poncirus trifoliata* and Jambheri.

Regulation of osmosis in roots and maintenance of passive water status under conditions of soil-water deficit had a positive influence on gas exchange. There was an increase in total root length and increased root-to-shoot-length ratio of the rootstocks Dog Ridge and Salt Creek at 50% stress compared with when under control conditions (data not shown). This increased root length in these rootstocks at 50% stress might have efficiently absorbed water from the lower soil surface and thus maintained a high RWC, resulting in better leaf and osmotic potential of the scion varieties budded on them. During (1994) also opined that the rate of photosynthesis of grapes might be maintained by the root system. Dehydration of part of the root led to stomatal closure and a decline in photosynthesis despite the maintenance of leaf turgor, indicating that the physiological effect of grafted vines is scion specific (Williams & Smith, 1991). Williams and Smith found that the assimilation rates of ungrafted vines were similar, but the rate was significantly higher when vines were grafted to Kober 5BB. The higher rate of photosynthesis was associated with significantly higher stomatal conductance. Likewise, in the present study, the higher WUE in a few scion/rootstock combinations may be due to interaction between rootstocks and scions. It is important to have an increased WUE (e.g. as in Flame Seedless and Sharad Seedless budded on Dog Ridge) under drought conditions rather than increased photosynthesis and a reduced transpiration rate. In some scion/rootstock combinations, e.g. Sharad Seedless budded on VC clone, at 50% stress there was a reduction in photosynthesis and an increase in transpiration, which resulted in lower water use efficiency. Some rootstocks can strongly influence plant response to low moisture in terms of reduced photosynthesis, stomatal conductance and internal CO_2 content in grape varieties (Iacono, 1998).

CONCLUSIONS

It is evident from the present study that budding Sharad Seedless on the rootstock Dog Ridge may be of relevance in increasing the photosynthesis potential. It is thus important to take genotypic selection of rootstocks into account. Dog Ridge and Salt Creek rootstocks had better tolerance levels compared with other rootstocks, such as VC clone, as indicated by the recorded physiological parameters under conditions of moisture stress when they were grown on their own roots (Satisha *et al*., 2004). Dog Ridge and Salt Creek rootstocks also influenced the physiological parameters of scion varieties Flame Seedless and Sharad Seedless in terms of enhancing WUE under moisture stress conditions. Results obtained in this study also showed that certain scion/rootstock combinations perform poorly under water stress conditions.

Therefore careful selection of rootstocks, which are known to influence the physiology of scion leaves with respect to drought tolerant characteristics, such as maintaining a higher RWC, leaf water potential, osmotic potential and increased WUE under water scarce conditions should be made when establishing vineyards in regions that experience water scarcity.

LITERATURE CITED

Barrs, H.D. & Weatherly, P.E., 1962. A re-examination of the relative turgidity technique for estimating water deficit in leaves. Agric. J. Biol. Sci. 15, 413-428.

Brown, C.S., Young, E. & Pharr, D.M., 1985. Rootstocks and scion effect on carbon partitioning in apple leaves. J. Am. Soc. Hort. Sci. 110, 701-705.

Bica, D., Gay, G., Mordano, A., Souve, E. & Bravdo, B.A., 2000. Effect of rootstocks and *Vitis vinifera* on photosynthetic parameters. Acta Hort. 526, 373-379.

During, H., 1994. Photosynthesis of grafted and ungrafted grape vines; Effect of rootstock genotypes and plant age. Am. J. Enol. Vitic. 45, 297-299.

Gomez, A.K. & Gomez, A.A., 1984. Statistical procedures for agricultural research. 2nd Edition. Wiley- Interscience, New York. pp:187-241.

Iacono, F., Bucella, A. & Peterlunger, E., 1998. Water stress and rootstock influence on leaf gas exchange of grafted and ungrafted grape vines. Sci. Hort. 75**,** 27-39.

Lincoln, T. & Eduardo, Z., 2002. Plant physiology (II ed). Sinauer Associates Publishers, Sunderband, Massachusetts. p: 792.

Nagarajah, S., 1989. Physiological responses of grape vines to water stress. Acta Hort., 240, 249-256.

Passioura, J.B., 1986. Resistance to drought and salinity: Avenues for crop improvement. Aust. J. Plant Physiol. 13**,** 191-201.

Satisha, J., Prakash, G.S., Bhatt, R.M. & Sampathkumar, P., 2004. Physiological mechanisms of water use efficiency in grape rootstocks under drought conditions. (Correspondence with Indian. J. Agril. Sci.)

Sharma, S.K. & Singh, R., 1989. Photosynthetic characters and productivity in citrus. II. Effect of rootstocks. Indian J. Hort. 46, 422-425.

Sobhana, P., 1988. Physiology of rooting and stock scion interactions in Hevea. PhD Thesis, Kerala Agriculture University, Kerala.

Souza, C.R., Soares, A.M., Regina, M. & Souza, D., 2001. Gas exchange of vine cuttings obtained from two graftings submitted to water deficiency. Pesquisa Agropecuaria Brasileira 36, 1221-1230.

Williams, L. & Smith, R.J., 1991. The effect of rootstocks on the partitioning of dry weight, nitrogen and potassium and root distribution of Cabernet Sauvignon grape vines. Aust. J. Enol. Vitic. 42, 118-112.

Zamboni, M. & Iacono, F., 1998. Study on variation in osmotic potential and cellular elasticity in vines subjected to water stress. Connaissance-de-la-vigne-et-du-vin, 22, 241-249.