Asian Journal of Plant Sciences

ISSN 1682-3974

science alert

ANSInet
an open access publisher
http://ansinet.com

Asian Journal of Plant Sciences 4 (4): 438-444, 2005
ISSN 1682-3974

Gas Exchange Responses of Oil Palm to *Ganoderma boninense* Infection

M.H. Haniff, S. Ismail and A.S. Idris
Malaysian Palm Oil Board, P.O. Box 10620, Kuala Lumpur, Malaysia

Abstract: A comparison of physiological parameters was carried out between healthy and *Ganoderma* infected 17-year old oil palms grown under the same field conditions. Results from gas exchange measurements indicate that stomatal conductance was significantly reduced in infected palms. This led to significant reductions in transpiration rate and intercellular CO_2 concentration in the infected palms. The relative leaf chlorophyll content and quantum efficiency of PS II were also significantly reduced in the infected palms. The results indicate that infected palms were under water stress that was induced by injury to their root and vascular transport system and not related to soil water deficits.

Key words: Oil palm, *Ganoderma boninense*, stomatal conductance, chlorophyll, transpiration, intercellular CO_2, chlorophyll fluorescence, quantum efficiency

INTRODUCTION

Basal stem rot in oil palm is caused by *Ganoderma boninense* and it is the most severe fungal disease of oil palm in Malaysia. It has the ability to infect oil palms from as young as 12-24 months[1] to over 24 years after field planting[2]. High incidences of this disease have been reported in oil palms planted on coastal soil and peat[3-5]. The incidence of *Ganoderma* in inland soils was relatively low and confined to waterlogged area[3]. However, Benjamin and Chee[6] reported the presence of disease on palms planted on lateritic soils that were previously disease free. Currently, there is no effective treatment for *Ganoderma* infected palms, while preventive measures undertaken show varying degrees of effectiveness. The mode of infection is through the oil palm root system and the disease has reached a critical stage by the time fruiting bodies or foliar symptoms are visible.

Like all fungi, *G. boninense* have no chlorophyll and thus, lack photosynthetic capability. Instead of manufacturing their own food, fungi absorb nutrients from either living or dead host tissue. Thus, parasitic fungi live off the host plant and endanger the host's health. Many saprophytic fungi can be weakly parasitic in their behavior, especially if their host is dying from other causes. *Ganoderma* is among one of these facultative parasites i.e., a saprophytic fungus activated by favorable conditions to behave parasitically[7]. Carbon assimilates produced by the host palm may be diverted to the sites of infection in response to wounding by the disease. This reduces the supply of carbon assimilates to other developing organs of the host palm, such as new leaves, roots and fruit bunches. *Ganoderma* infection can also affect the absorption and translocation of water and nutrients throughout the host palm. The disruption is due to destruction of the root system, blockage of water and nutrient movement in the xylem or phloem, or the redirection of host nutrients[8].

In general, plant disease can alter the normal physiology of a plant, which includes many processes such as photosynthesis, respiration, absorption and translocation of water and nutrients, transport of photosynthetic products and production of growth compounds. Some responses to infection occur at the leaf level in response to stimuli generated in the leaf itself or elsewhere in the plant. They have a negative influence on carbon assimilation and growth. However, it is the integrated response at the whole plant level, including carbon assimilation and the allocation of photoassimilates to different plant parts and reproductive ability that finally dictates survival and persistence under environmental stress[9].

Conditions that reduce the absorption of water and nutrients will have a tendency to impose stress on the palm and affect its ability to carry out photosynthesis. However, when light, nutrients and water are non-limiting, CO_2 availability is more often a limiting factor in the photosynthesis process. Other environment factors that could influence photosynthesis through regulation of stomatal conductance are vapour pressure deficit and temperature[10]. Infected palms are expected to show differences in physiological activity at the leaf level as compared to healthy palms, when grown under the same environmental conditions. This study was undertaken to

Corresponding Author: Dr. M.H. Haniff, Senior Research Officer, Biology Division, Malaysian Palm Oil Board, No. 6, Persiaran Institusi, BB Bangi, 43000 Kajang, Selangor, Malaysia
Tel: 603-89259155 Fax: 03 89258215

investigate the effects of *Ganoderma* infection on gas exchange characteristics of field planted oil palms in Malaysia.

MATERIALS AND METHODS

The study was carried out at an experimental field trial at the MPOB Research Station in Kluang, Johor. The field was planted in September 1986 with DxD (Serdang) palms on lateritic soil at 148 palms per hectare and received the standard estate management practice. Palms are considered healthy when they still have intact frond canopy and no fungal fruiting bodies on their trunk, while infected palms had *Ganoderma* fruiting bodies on their trunk. In January 2003, five palms with uniform vegetative appearance (i.e. at least 25 to 30 green fronds per palm) were selected from healthy and infected groups. A 3m scaffolding tower was used to reach the frond leaflets for gas exchange measurements. Measurements were taken from fronds 1, 9 and 17 of each selected palm.

Gas exchange measurements: Gas exchange characteristics were measured of 6 upper rank leaflets from the middle region of the chosen frond using a portable photosynthesis system (CIRAS-1, PP-System, UK). The leaf cuvette was controlled at 350 ppm CO_2, 30°C, 70% relative humidity and 1000 μM m^{-2} sec^{-1} Photosynthetically Active Radiation (PAR). Measurements were made between 9 am to 2 pm and completed within 5 days. A pair of healthy and infected palms was measured at each day.

Relative chlorophyll content and chlorophyll fluorescence measurements: Relative chlorophyll content of leaves was determined by a chlorophyll meter (SPAD 502, Minolta, Japan). Quantum efficiency of photosystem II ($\Phi_{PS\ II}$) was determined with a portable chlorophyll fluorescence meter (FMS 2, Hansatech, UK). Measurements were made at the same time as the gas exchange measurements.

RESULTS AND DISCUSSION

Photosynthesis: Photosynthetic rates measured from fronds of different ages showed no significant difference between healthy and infected palms (Table 1). Both showed decreasing photosynthetic rates with increasing frond age that can be attributed to leaf senescence, position in the canopy or both. Infected palms had a non-significant 13% reduction in mean photosynthetic rate as compared to healthy palms (Table 2). Photosynthesis is limited primarily by light harvesting and

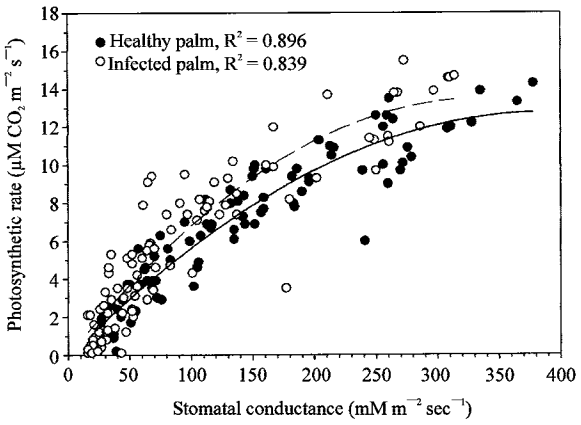

Fig. 1: Relationship between stomatal conductance and photosynthetic rate of healthy and infected palms

assimilatory power under low light and by carboxylation and photorespiration under low CO_2. However, under saturating light and CO_2, photosynthesis may be controlled by processes that convert triose-phosphate into starch and sucrose[11-13]. Carbon assimilation also decreases as a consequence of limitations to CO_2 diffusion in the leaf, diversion of carbon allocation to non-photosynthetic organs and production of defense molecules, or changes in leaf biochemistry that result in the down regulation of photosynthesis. The photosynthetic rate (A) of both C_3 and C_4 plants also decreases as their relative water content and water potential decrease[14-17]. In C_3 species such as the oil palm, Rubisco capacity is the primary limitation to A at light saturation and with CO_2 concentrations below the ambient atmospheric value (350 ppm), particularly near the temperature optimum. Photosynthesis rates also decrease with reduction in stomatal conductance[18].

Stomatal conductance: The stomatal conductance (g_s) was significantly reduced at all frond ages in infected, as compared to healthy palms (Table 1). There was a reduction of about 30.5% in the mean stomatal conductance of the infected palms as compared to healthy palms (Table 2). This implies that the infected palms experience stress that triggers their stomata to partially close. The stress was mainly due to the infection since the palms were under the same environmental conditions. However, the mean stomatal conductance value for the infected palms was still adequate to support gas exchange as indicated by the photosynthetic rates. There was a strong relationship between A and g_s for both healthy and infected palms (Fig. 1). There is often a close relationship between g_s and A[19], because an early and progressive effect of water stress is stomatal closure[14,15,17,20-22].

Table 1: Gas exchange, relative leaf chlorophyll content and PS II quantum efficiency of different fronds from healthy and infected palms

		Frond No.		
Measurements	Palm status	1	9	17
Photosynthesis (μM CO_2 m^{-2} sec^{-1})	Healthy	7.87±0.62Aa	6.95±0.70Aab	6.04±0.74Ab
	Infected	6.47±0.85Aa	6.63±0.71Aab	4.75±0.75Ab
Stomatal conductance (mM m^{-2} sec^{-1})	Healthy	154.48±15.72Aa	146.73±16.72Aa	136.43±18.77Aa
	Infected	95.67±17.10Ab	108.27±14.30Ba	98.10±15.88Ba
Transpiration (mM H_2O m^{-2} sec^{-1})	Healthy	2.35±0.18Aa	2.11±0.19Aa	1.93±0.20Aa
	Infected	1.52±0.21Ba	1.76±0.19Ba	1.56±0.20Ba
Intercellular CO_2 (ppm)	Healthy	206.69±3.12Aa	219.30±5.56Ab	222.57±6.59Ac
	Infected	172.23±9.39Ba	195.77±8.85Bb	226.83±7.49Bc
Relative leaf chlorophyll content (SPAD)	Healthy	63.08±1.81Aa	69.77±1.19Ab	71.84±1.31Ab
	Infected	56.68±1.48Ba	61.94±1.24Bb	64.93±1.38Bb
PS II quantum efficiency	Healthy	0.76±0.01Aa	0.72±0.03Aa	0.72±0.02Aa
	Infected	0.71±0.01Ba	0.71±0.01Ba	0.68±0.02Ba

Column means±S.E. followed by the same capital letter and row means±S.E. followed by the same small letter(s) are not statistically significant at $p<0.05$

Table 2: Mean gas exchange parameters measured of healthy and infected palms

Palms	Photosynthetic rates (μM CO_2 m^{-2} sec^{-1})	Stomatal conductance (mM m^{-2} sec^{-1})	Transpiration rates (mM H_2O m^{-2} sec^{-1})	Intercellular CO_2 (ppm)	C_i/C_a
Healthy	6.9±0.4a	144.9±9.7a	2.1±0.1a	215.8±3.1a	0.62±0.01a
Infected	6.0±0.4a	100.7±9.0b	1.6±0.1b	198.3±5.5b	0.57±0.02b
% reduction	13.0	30.5	23.9	8.1	8.0

Column mean±S.E. followed by the same letter are not statistically significant at $p<0.05$.

Light-saturated stomatal conductances have been used to reflect water stress intensity and are less dependent on the species and other environmental conditions. Many photosynthetic parameters, such as electron transport rate, carboxylation efficiency, intrinsic water-use efficiency and respiration rate in the light are also strongly correlated with stomatal conductance than with water status itself. In grapevines, non-stomatal limitations become important when g_s drop below 100-150 mM m^{-2} sec^{-1}. Under moderate water deficit, i.e. when photosynthesis is mainly limited by stomatal conductance, a complete recovery of the maximum A occurred one night after irrigation[23,24]. However, when the g_s value is less than 50 mM m^{-2} sec^{-1}, photosynthesis does not reverse even after irrigation[25]. Further reduction of g_s as water stress increases leads to reduced photosynthetic activity.

As water stress progresses, stomatal closure occurs for increasingly longer periods of the day in field-grown plants, beginning in mid-morning[26]. This depression in gas exchange simultaneously reduces daily carbon assimilation and water loss at the time of highest evaporative demand in the atmosphere and leads to a near optimization of carbon assimilation in relation to water supply[27,28]. The causes for this depression in net carbon uptake are still not fully understood and seem to involve mechanisms at both the stomatal[29] and chloroplastic level[30].

Transpiration rate (E): Leaf transpiration rate measured in the leaf cuvette was significantly reduced in infected palms by about 23.9% as compared to healthy palms (Table 1 and 2). This can be attributed to the lower stomatal conductance value of the infected palms, which reduces water loss from the leaves. CO_2 assimilation is closely related to leaf transpiration rate through the simultaneous flow of water vapor through the stomata to the atmosphere and CO_2 flow from the atmosphere into the leaf. Leaf transpiration is affected by leaf water content and influence the heat balance, which may influence the photosynthetic rate. The water status of the leaf has a pronounced effect on the stomatal conductance.

Stomatal control of water loss has been identified as an early event in plant responses to water deficit under field conditions, leading to a limitation of carbon uptake by the leaves[14,15]. Stomata close in response to either a decline in leaf turgor, leaf water potential or both[31], or to a low-humidity atmosphere[10,32,33]. Various experiments have shown that stomatal responses are often more closely linked to soil moisture content than to leaf water status. This suggests that stomata are responding to chemical signals, such as abscisic acid (ABA) produced by dehydrating roots, even when leaf water status is kept constant[34,35]. Although most evidence for this kind of response has been obtained under controlled conditions on small plants grown in containers[34,36], experiments with field-grown plants, such as maize[37], grapevine[38,39] and clover[40], also support this hypothesis. Much is known about the role of ABA in closing stomata, as well as its production in dehydrating roots and its circulation in the plant. However, there is still limited knowledge about the exact relationship between water deficit and ABA long distance signaling and the nature of interactions between ABA and other chemical signals, such as cytokinins and ethylene[41]. In mature trees, where long-distance transport of the chemical signal from the roots to the shoots would

be required, the evidence is even less clear[36]. Changes in plant hydraulic conductivity have been thought to play a major role in short-term stomatal regulation of woody plants[42]. The interactions between root chemical signaling and changes in plant hydraulic conductivity during drought remain vague and need further consideration[43].

Intercellular CO_2 concentration: The intercellular CO_2 concentration (C_i) in the infected palms was significantly reduced by about 8.1% compared with healthy palms (Table 2). However, no significant increase in C_i value was observed in frond 17 of the infected palms (Table 1). The higher C_i value of frond 17 was probably cause by the lower stomatal conductance and high leaf respiration rate. Leaf respiration continues after photosynthesis starts to decline since mitochondria remain intact[44]. C_3 leaves exposed to high temperature often maintain intercellular CO_2 levels that fall on the initial slope of the photosynthetic CO_2 response curve[12,45]. This is a region commonly thought to reflect a limitation in rubisco capacity. Rubisco also deactivates at high temperature in C_3 species[45-47]. The C_i has also been shown in previous studies to be more dependent on g_s than on leaf water potential[23,24]. The strong relationship between A and g_s also indicates that reduction in the transpiration rate and intercellular CO_2 concentration was regulated mostly by stomatal closure.

The ratio of internal to atmospheric CO_2 concentration (C_i/C_a) in infected palms was reduced by about 8% as compared to healthy palms (Table 2). As stomata close, the CO_2 concentration inside the leaf initially declines with increasing stress and then increases as water stress becomes more severe[17,48]. After an early partial closure of stomata, metabolic limitation, caused by either damage (i.e. permanent) or adjustment (i.e. reversible down-regulation) occurs.

Relative leaf chlorophyll content: The relative leaf chlorophyll (Chl) content was significantly reduced in the infected palms by about 10.3% as compared to healthy palms (Table 3). It also increased with increasing frond age (Table 1). Chlorophyll is the molecule that absorbs light and uses the energy to synthesize carbohydrates from CO_2 and water. Reductions in leaf Chl content can affect light use efficiency and CO_2 assimilation. Previous research indicates a close correlation between leaf Chl content and leaf nitrogen (N) content. This is because much of leaf N is contained in Chl[49]. Both decreased and unchanged Chl levels during drought stress have been observed in other plant species, depending on drought duration and severity[50-52]. Plants subjected to water

Table 3: Mean relative leaf chlorophyll content and quantum efficiency of PS II of healthy and infected palms

Palms	Relative leaf chlorophyll content (SPAD)	Quantum efficiency PS II
Healthy	68.23±0.94a	0.73±0.01a
Infected	61.18±0.85b	0.70±0.01b
% reduction	10.3	4.1

Column means±S.E. followed by the same letter are not statistically significant at $p<0.05$

shortage can have accelerated leaf senescence because it reduces the water demand and allows recycling of scarce resources to the reproductive sinks[53]. During leaf senescence, a large part of the leaf nitrogen, carbon and minerals is recycled to other organs of the plant[54]. However, early leaf senescence will reduce crop yield because cumulative photosynthesis is reduced[55,56].

Quantum efficiency PS II: Quantum efficiency of PS II ($\Phi_{PS\ II}$) was significantly reduced in the infected palms by about 4.1% as compared to healthy palms (Table 2). It also tended to decrease with increasing frond age (Table 1). The lower $\Phi_{PS\ II}$ value in the infected palms implies that their light use efficiency was affected, since the fluorescence measurement reflects changes in the efficiency with which absorbed light is used for PS II photochemistry. In healthy leaves, this value is always close to 0.8, independently of the plant species studied. A lower value indicates that a proportion of PS II reaction centers are damaged, a phenomenon called photoinhibition, often observed in plants under stress conditions[57,58]. Chlorophyll fluorescence also showed a high dependency on stomatal conductance.

In perennial crops such as the oil palm, the dissipation of excitation energy at the chloroplast level through processes other than photosynthetic carbon-metabolism is an important defense mechanism under conditions of water stress and is accompanied by down-regulation of photochemistry and, in the longer term, of photosynthetic capacity and growth.

When water deficit develops slowly, one of the first events to take place in plants is stomatal closure in response to the migration of chemical compounds synthesized in dehydrating roots (e.g. ABA). The decline in intercellular CO_2 following stomatal closure and the lower light use efficiency under drought may induce, in the long-term, a down-regulation of the photosynthetic machinery to match the available carbon substrate.

Ganoderma infection strongly affected the leaf gas exchange of oil palms through a reduction in stomatal conductance, which led to a significant reduction in transpiration rates and intercellular CO_2 levels. Infected palms had lower relative leaf chlorophyll content and lower quantum efficiency of PS II. These responses imply that infected palms were subjected to water stress as a

result of *Ganoderma* induced injury to the root and vascular transport systems. The stress was not related to soil water deficits since the palms were grown under the same environmental conditions. This information is useful for developing a suitable method for early detection of *Ganoderma* infection in oil palm. Further research is needed to ascertain the physiological mechanisms involved, particularly during the initial stage of infection.

ACKNOWLEDGMENTS

We wish to thank the Director General of MPOB for permission to publish this work, Mr. Maurad Ahmad and Mr. Abdullah Badrishah for technical assistance, Mr. Zaki Aman for logistic support and Dr. I.E. Henson, Dr. Ariffin Darus and Dr. Norman Kamaruddin for useful comments on the manuscript.

REFERENCES

1. Singh, G., 1990. *Ganoderma*-the Scourge of Oil Palm in the Coastal Area. In: Ariffin, D. and S. Jalani (Eds.). Proc. *Ganoderma* Workshop, 11 September 1990, Palm Oil Research Institute of Malaysia, Bangi, Selangor, Malaysia, pp: 7-35.
2. Thompson, A., 1931. Stem-rot of the oil palm in Malaya. Bulletin Straits Settlement and FMS., Science Series, 6: 23.
3. Khairudin, H., 1990. Results of Four Trials on *Ganoderma* Basal Stem Rot of Oil Palm in Golden Hope Estates. In: Ariffin, D. and S. Jalani (Eds.). Proc. *Ganoderma* Workshop, 11 September 1990, Palm Oil Research Institute of Malaysia, Bangi, Selangor, Malaysia, pp: 67-80.
4. Ariffin, D., A.S. Idris and D. Mohd Tayeb, 1989. Approach to Controlling of *Ganoderma* on Oil Palm in Malaysia. In: Proc. 1989 Intl. Conf. Palms and Palm Products, 21-25 November 1989, Benin City, Nigeria. Paper No. 55.
5. Ariffin, D. and A.S. Idris, 2003. Progress and Research on *Ganoderma* Basal Stem Rot of Oil Palm. In: Mohd Basri, W., K.W. Chan, D. Mohd Tayeb and S. Sundram (Eds.). Proc. Seminar on Elevating National Oil Palm Productivity and Recent Progress in the Management of Peat and *Ganoderma*. Malaysian Palm Oil Board, Bangi, Selangor, Malaysia, pp: 167-205.
6. Benjamin, M. and K.H. Chee, 1995. Basal stem rot of oil palm-a serious problem on inland soils. MAPPS Newslett., 19: 3.
7. Stamets, P., 2004. The Role of Mushrooms in Nature. In: Elevitch, C.R., (Ed.). The Overstory Book: Cultivating Connections with Trees, 2nd Edn. Permanent Agriculture Resources, USA., pp: 74-80.
8. Riley, M.B., 2003. Disruption of Plant function. In: Trigiano, R.N., M.T. Windham and A.S. Windham (Eds.). Plant Pathology: Concepts and Laboratory Exercises. CRC Press, UK., pp: 265-274.
9. Pereira, J.S. and M.M. Chaves, 1993. Plant Water Deficits in Mediterranean Ecosystems. In: Smith, J.A.C. and H. Griffiths (Eds.). Plant Responses to Water Deficits-from Cell to Community. BIOS Scientific Publishers Ltd., Oxford, pp: 237-251.
10. Henson, I.E., 1991. Limitations to Gas Exchange, Growth and Yield of Young Oil Palm by Soil Water Supply and Atmospheric Humidity. Trans. Malaysian Soc. Plant Physiol., 2: 51-57.
11. Sage, R.F., T.D. Sharkey and J.R. Seemann, 1990. Regulation of ribulose-1,5-bisphosphate carboxylase activity in response to light intensity and CO_2 in the C_3 annuals *Chenopodium album* L. and *Phaseolus vulgaris* L. Plant Physiol., 94: 1735-1742.
12. Sage, R.F., 1994. Acclimation of photosynthesis to increasing atmospheric CO_2: The gas exchange perspective. Photosynthesis Res., 39: 351-368.
13. Stitt, M., 1996. Metabolic Regulation of Photosynthesis. In: Baker, N.R., (Ed.). Photosynthesis and the Environment. Kluwer Academic Publishers, The Netherlands, pp: 151-190.
14. Chaves, M.M., 1991. Effects of water deficits on carbon assimilation. J. Exp. Bot., 42: 1-16.
15. Cornic, G. and A. Massacci, 1996. Leaf Photosynthesis under Drought Stress. In: Baker, N.R., (Ed.). Photosynthesis and the Environment. New York: Kluwer Academic Publishers, The Netherlands, pp: 347-366.
16. Kramer, P.J. and J.S. Boyer, 1995. Water Relation of Plants and Soils. Academic Press, San Diego, pp: 495.
17. Lawlor, D.W., 1995. The Effects of Water Deficit on Photosynthesis. In: Smirnoff, N., (Ed.). Environment and plant metabolism. Bios Scientific Publishers, Oxford, pp: 129-160.
18. Siddique, M.R.B., A. Hamid and M.S. Islam, 1999. Drought stress effects on photosynthetic rate and leaf gas exchange of wheat. Bot. Bull. Acad., 40: 141-145.
19. Wong, S.C., I.R. Cowan and G.D. Farquhar, 1979. Stomatal conductance correlates with photosynthetic capacity. Nature, 282: 424-426.
20. Boyer, J.S., 1976. Photosynthesis at low water potentials. Philosophical Trans. Royal Soc., 273: 501-512.
21. Ort, D.R., K. Oxborough and R.R. Wise, 1994. Depressions of Photosynthesis in Crops with Water Deficits. In: Baker, N.R. and J.R. Bowyer (Eds.). Photoinhibition of photosynthesis from molecular mechanisms to the field. BIOS Scientific Publishers Ltd., Oxford, pp: 315-329.

22. Sharkey, T.D., 1990. Water stress effects on photosynthesis. Photosynthetica, 24: 651.
23. Flexas, J., J.M. Escalona and H. Medrano, 1998. Down-regulation of photosynthesis by drought under field conditions in grapevine leaves. Aust. J. Plant Physiol., 25: 893-900.
24. Flexas, J., J.M. Escalona and H. Medrano, 1999. Water stress induces different levels of photosynthesis and electron transport rate regulations in grapevines. Plant Cell Environ., 22: 39-48.
25. Quick, W.P., M.M. Chaves, R. Wendler, M.M. David, M.L. Rodrigues, J.A. Passarinho, J.S. Pereira, M.D. Adcok, R.C. Leegood and M. Stitt, 1992. The effect of water stress on photosynthetic carbon metabolism in four species grown under field conditions. Plant Cell Environ., 15: 25-35.
26. Tenhunen, J.D., R.W. Pearcy and O.L. Lange, 1987. Diurnal Variations in Leaf Conductance and Gas Exchange in Natural Environments. In: Zeiger, E., G.D. Farquhar and I.R. Cowan (Eds.). Stomatal function. Stanford University Press, Stanford, pp: 323-51.
27. Cowan, I.R., 1981. Regulation of Water Use in Relation to Carbon Gain in Higher Plants. In: Lange, O.L., P.S. Nobel, C.B. Osmond and H. Ziegler (Eds.). Physiological Plant Ecology II. Water relations and Carbon Assimilation. Encyclopaedia of Plant Physiology Vol. 12B. Berlin, Springer, pp: 589-614.
28. Jones, H.G., 1992. Plants and microclimate: A Quantitative Approach to Environmental Plant Physiology. 2nd Edn. Cambridge University Press, Cambridge, England, pp: 428.
29. Downton, W.J.S., B.R. Loveys and W.J.R. Grant, 1988. Non-uniform stomatal closure induced by water stress causes putative non-stomatal inhibition of photosynthesis. New Phytologist, 110: 503-509.
30. Correia, M.J., M.M.C. Chaves and J.S. Pereira, 1990. Afternoon depression in photosynthesis in grapevine leaves-evidence for a high light stress effect. J. Exp. Bot., 41: 417-426.
31. Ludlow, M.M., 1980. Adaptive Significance of Stomatal Responses to Water Stress. In: Turner N.C. and P.J. Kramer (Eds.). Adaptation of Plants to Water and High Temperature Stress. Wiley, New York, pp: 123-138.
32. Maroco, J.P., J.S. Pereira and M.M. Chaves, 1997. Stomatal responses to leaf-to-air vapour pressure deficit in Sahelian species. Aust. J. Plant Physiol., 24: 381-387.
33. Schulze, E.D., 1986. Carbon dioxide and water vapour exchange in response to drought in the atmosphere and in the soil. Ann. Rev. Plant Physiol., 37: 247-274.
34. Davies, W.J. and J. Zhang, 1991. Root signals and the regulation of growth and development of plants in drying soil. Ann. Rev. Plant Physiol., 42: 55-76.
35. Gowing, D.J.G., W.J. Davies and H.G. Jones, 1990. A positive root-source signal as an indicator of soil drying in apple, *Malus domestica*. J. Exp. Bot., 41: 1535-1540.
36. Jackson, G.E., J. Irvine, J. Grace and A.A.M. Khalil, 1995. Abscisic acid concentrations and fluxes in droughted conifer saplings. Plant Cell Environ., 18: 13-22.
37. Tardieu, F., N. Katerji, J. Bethenod, J. Zhang and W.J. Davies, 1991. Maize stomatal conductance in the field: Its relationship with soil and plant water potentials, mechanical constraints and ABA concentration in the xylem sap. Plant Cell and Environ., 14: 121-126.
38. Correia, M.J., J.S. Pereira, M.M. Chaves, M.L. Rodrigues and C.A. Pacheco, 1995. ABA xylem concentration determines maximum daily leaf conductance of field-grown *Vitis vinifera* L. plants. Plant Cell Environ., 18: 511-521.
39. Stoll, M., B. Loveys and P. Dry, 2000. Hormonal changes induced by partial rootzone drying of irrigated grapevine. J. Exp. Bot., 51: 1627-1634.
40. Socias, X., M.J. Correia, M.M. Chaves and H. Medrano, 1997. The role of abscisic acid and water relations in drought responses of subterranean clover. J. Exp. Bot., 48: 1281-1288.
41. Sauter, A., W.J. Davies and W. Hartung, 2001. The long-distance abscisic acid signal in the droughted plant: The fate of the hormone on its way from root to shoot. J. Exp. Bot., 52: 1991-1998.
42. Saliendra, N.Z., J.S. Sperry and J.P. Comstock, 1995. Influence of leaf water status on stomatal response to humidity, hydraulic conductance and soil drought in *Betula occidentalis*. Planta, 196: 357-366.
43. Jackson, R.B., J.S. Sperry and T.E. Dawson, 2000. Root water uptake and transport: Using physiological processes in global predictions. Trends Plant Sci., 5: 482-488.
44. Collier, D.E. and B.A. Thibodeau, 1995. Changes in respiration and chemical content during autumnal senescence of *Populus tremuloides* and *Quercus rubra* leaves. Tree Physiol., 15: 759-764.
45. Sage, R.F., T.D. Sharkey and R.W. Pearcy, 1990. The effect of leaf nitrogen and temperature on the CO_2 response of photosynthesis in *Chenopodium album* L., a C_3 dicot. Aust. J. Plant Physiol., 17: 135-148.
46. Kobza, J. and G.E. Edwards, 1987. Influences of leaf temperature on photosynthetic carbon metabolism in wheat. Plant Physiol., 83: 69-74.

47. Vu, J.C.V., L.H. Allen, K.J. Boote and G. Bowes, 1997. Effects of elevated CO_2 and temperature on photosynthesis and rubisco in rice and soybean. Plant Cell Environ., 20: 68-76.
48. Henson, I.E., Z.M. Jamil and M.T. Dolmat, 1993. Regulation of gas exchange and abscisic acid concentrations in young oil palm (*Elaeis guineensis*). Trans. Malaysian Soc. Plant Physiol., 3: 29-34.
49. Jiang, Y. and B. Huang, 2001. Drought and heat stress injury to two cool-season turfgrasses in relation to antioxidant metabolism and lipid peroxidation. Crop Sci., 41: 436-442.
50. Jagtap, V., S. Bhargava, P. Streb and J. Feierabend 1998. Comparative effect of water, heat and light stresses on photosynthetic reactions in *Sorghum bicolor* (L.) Moench. J. Exp. Bot., 49: 1715-1721.
51. Rensburg, L.V. and G.H.J. Kruger, 1994. Evaluation of components of oxidative stress metabolism for use in selection of drought tolerant cultivars of *Nicotiana tabacum* L.J. Plant Physiol., 143: 730-737.
52. Zhang, J. and M.B. Kirkham, 1996. Antioxidant responses to drought in sunflower and sorghum seedlings. New Phytologist, 132: 361-373.
53. Pic, E., B.T. de La Serve, F. Tardieu and O. Turc, 2002. Leaf senescence induced by mild water deficit follows the same sequence of macroscopic, biochemical and molecular events as monocarpic senescence in pea. Plant Physiol, 128: 236-246.
54. Nooden, L.D., 1988. The Phenomena of Senescence and Aging. In: Noodén, L.D. and A.C. Leopold (Eds.). Senescence and Aging in Plants. Academic Press Inc., San Diego, pp: 1-50.
55. Gifford, R.M. and C.L.D. Jenkins, 1982. Prospects for Applying Knowledge of Photosynthesis Toward Improving Crop Production. In: Govindjee, (Ed.). Photosynthesis, Vol. 2. Academic Press Inc., New York, pp: 419-457.
56. Wolfe, D.W., D.W. Henderson, T.C. Hsiao and A. Alvino, 1988. Interactive water and nitrogen effects on senescence of maize. I: Leaf area duration, nitrogen distribution and yield. Agron. J., 80: 859-864
57. Govindjee, 1995. 63 years since kautsky-chlorophyll-a fluorescence. Aust. J. Plant Physiol., 22: 711-711.
58. Maxwell, K. and G.N. Johnson, 2000. Chlorophyll fluorescence-a practical guide. J. Exp. Bot., 51: 659-668.