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Effects of Vapour Pressure Difference on CO_2 Assimilation Rate, Leaf Conductance and Water Use Efficiency in Grass Species

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To compare the effect of air humidity (leaf-to-air vapour pressure difference, VPD) on net CO, assimilation rate, leaf conductance and water use efficiency for leaves of C_3 and C_4 grass species, rates of photosynthesis and transpiration were measured under different conditions of VPD and irradiance using a climate-controlled assimilation chamber. Four C_3 species and fourteen C_4 species were used as materials. All species measured showed a decrease in leaf conductance with increasing VPD, but the decreasing rate of the C_3 species was larger than that of the C_4 species. This shows that the stomata of C_3 species is more sensitive to VPD as compared with the C_4 species, The CO, assimilation rate of C_3 and C_4 species were also decreased with increasing VPD, but the percentage of the reduction was larger in the C_3 species than in the C_4 species. The response of water use efficiency to VPD was larger in the C_4 species than in the C_3 species, There were a marked positive correlations between leaf conductance and CO, assimilation rate in both type species, but the slope of the regression line of the C_4 species was twice of that of C_3 species at the lower range of leaf conductance (below 300 mmol $m^{-2} s^{-1}$). The stomata1 frequency of C_3 species was greater than that of C_4 species. The differences in the stomata1 sensitivity between C_3 and C_4 species to VPD were discussed in relation to the differences in the stomata1 frequency.

INTRODUCTION

It has become apparent that the leaf conductance of many species are sensitive to change in vapour pressure difference (VPD) between the inside of the leaf and the ambient air. However, the mechanisms by which VPD affects the leaf conductance and net CO, assimilation rate are unclear (Farquhar and Sharkey, 1982 ; Forseth and Ehleringer, 1983 ; Morison and Gifford, 1983). In some of the plants, for example, transpiration rate was observed to decline and leaf water potential increase with increasing VPD (West and Gaff, 1976 ; Schulze, 1972). These types of response cannot to be explained by negative feedback hypothesis involving change in bulk leaf water status. Stomata1 closure and consequent decrease in leaf conductance at high VPD is, therefore, thought to be a result from a water deficits somewhere in the epidermis, because of water loss from the leaf not controlled by the stomata (Turner *et al., 1984).* In other words, the variation in stomata1 aperture seems almost entirely due to a direct response to the VPD (Lösch, 1979 ; Schulze and Hall, 1982). Farquhar (1978) and Farquhar *et al.* (1980) termed this type of response as a “feedforward” and then proposed that peristomatal transpiration, direct evaporation from the external cuticle and subsidiary cells, was the only mechanism consistent with the feedforward response. Maier-Maercker (1983) comprehensively reviewed the role of peristomatal transpiration in relation to the mechanism of stomatal movement. From the information it is evident that direct stomatal responses to humidity act to conserve water and inhibit development of severe leaf water deficits, but their full importance in terms of control of water use efficiency has not been evaluated.

The objectives of the present study were to make clarify the stomatal responses in grass species to change in VPD and to examine the correlation between the stomatal response and stomatal frequency with special reference to the C_3 and C_4 photosynthetic properties.

MATERIALS AND METHODS

Four C_3 species, *Arundo donax, Oryza* ***sativa*** L. cv. Norin No. 21, 0. ***sativa*** L. cv. Nagakurabozu, 0. ***sativa*** L. cv. Norin No. 18, 0. ***sativa*** L. cv. Nihonbare, ***Hymenackne*** *indica* and *Phalaris* ***arundinacea*** and fourteen C_4 species, *Arundinella* ***kirta,*** *Brachiaria brazantha, Chenchrus ciliaris, Eleusine* ***coracana,*** *Eragrostis ferruginea, Hyparrhenia* ***rufa, Panicum antidotale, P. coloratum*** var. Kabulabula, ***P. coloratum*** var, Makariense, *P. dichotmiflorum,* ***P. maximum*** var. Maximum, *Paspalum dilatum, Setaria italica,* ***Sorghum bicolor*** and S. ***sudanense*** were studied. All species were grown from seed (except for ***A.*** *donax,* which was transplanted from an adjacent habitat) in 10 liter plastic pots filled with sandy loam soil and contained 10 g of compound chemical fertilizer (N : P : K ; 16 : 16 : 16). The plants were watered daily as needed to maintain adequate soil moisture levels. But the rice plants were maintained under submerged soil water conditions. Seeds were sown in July and grown outdoors, and measurements were performed at the vegetative stage in August and September.

Rates of CO, assimilation and transpiration were simultaneously measured by using a climate-controlled assimilation chamber. Detailes of gas exchange system and methods have been described previously (Agata *et* ***al.,*** 1986). Measurements were made on fully expanded young attached leaves. Enclosed leaf area was 50-70 cm^2. Parts of the plants outside the chamber were at the same irradiance as the leaf in the chamber. Light was provided by metal-halide lamps (Toshiba, Model D-400) filtered through approximately 15 cm of continously flowing water. Irradiance was varied by changing the distance between the lamps and the chamber, and measured with LI-COR quantum sensor (LI-COR Inc., Lincoln, Nebraska).

In order to measure the multiple effects of vapour pressure difference (VPD) and irradiance on leaf gas exchange, 0. ***sativa*** L. cv. Norin No. 18 for C_3 species and *P.* ***maximum*** var. Maximum for C_4 species were used as a representative from each type species. Experiments were initiated at high VPD and it was lowered in five steps allowing sufficient time for rates of gas exchange to become steady state after each change. In the current system, changes in VPD were completed at least within 40 min. At each step of VPD, irradiance was increased or decreased in four steps between 200 and 1800 $\mu E\,m^{-2}\,s^{-1}$. Steady rate of gas exchange and constant leaf temperature were achieved between 10 and 30 min after a change in irradiance, depending on species. Measurements were made at 30°C of leaf temperature and with $330 \pm 5\,\mu l\,l^{-1}$ ambient concentration of CO,.

For measuring the responses of leaf gas exchange to VPD under constant quantum flux density (2000 μE $m^{-2}s^{-1}$) in many grass species, two humidity controllers were used, the first one to regulate high humidity and the other to regulate low humidity. Experiments were started from high humidity, then humidity in the chamber was immediately decreased by changing the entering way of the air stream. Thereafter, humidity was increased to the same value as the humidity obtained at the beginning. Sufficient time was allowed at each step for steady state gas exchange rates to be established. All experiments were carried out at a constant leaf temperature of 30°C.

Rates of CO, assimilation and of transpiration, leaf conductance to water vapour, and intercellular CO, concentration were calculated from measured data according to

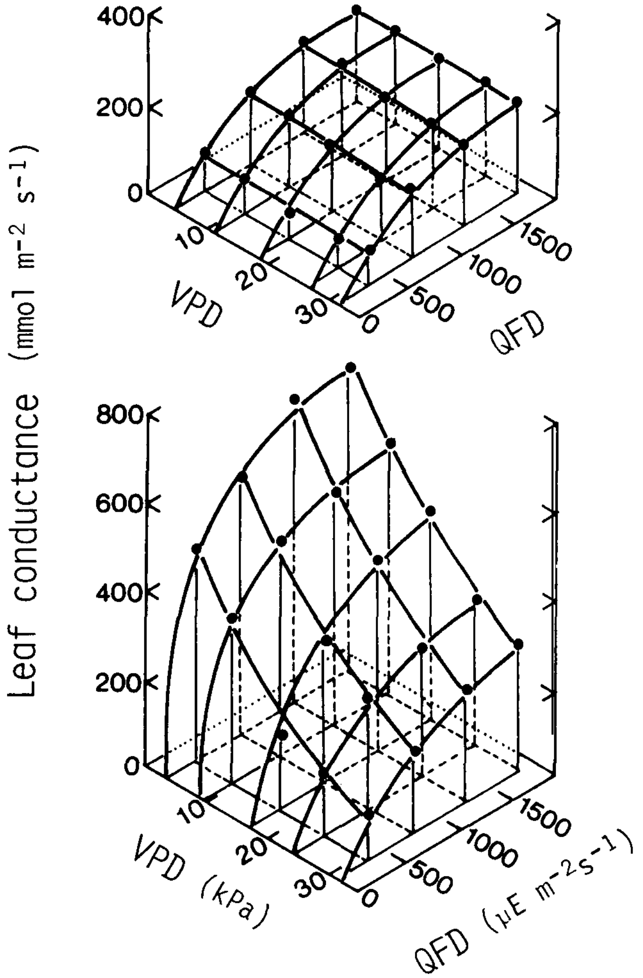

Fig. 1. Effects of vapour pressure difference (VPD) and quantum flux density (QFD) on leaf conductance in C_4 species (*P. maximum* var. Maximum, upper) and C_3 species (0. *sativa* L. cv. Norin No. 18, lower).

the equations of von Caemmerer and Farquhar (1981). The area of one side of the leaf enclosed was considered in the calculations. All measurements were made for two individuals per species or varieties.

After gas exchange measurements were complete, the stomatal frequency and the length of the guard cells (long axis) were measured with a light microscope.

RESULTS

Leaf conductance as functions of leaf-to-air vapour pressure difference (VPD) and irradiance for C_3 species (0. *sativa* L. cv. Norin No. 18) and C_4 species (*P. maximum* var. Maximum) could be expressed in the form of a three-dimensional graph as shown in Fig. 1. In the C_3 species, increase in irradiance and decrease in VPD led to a larger

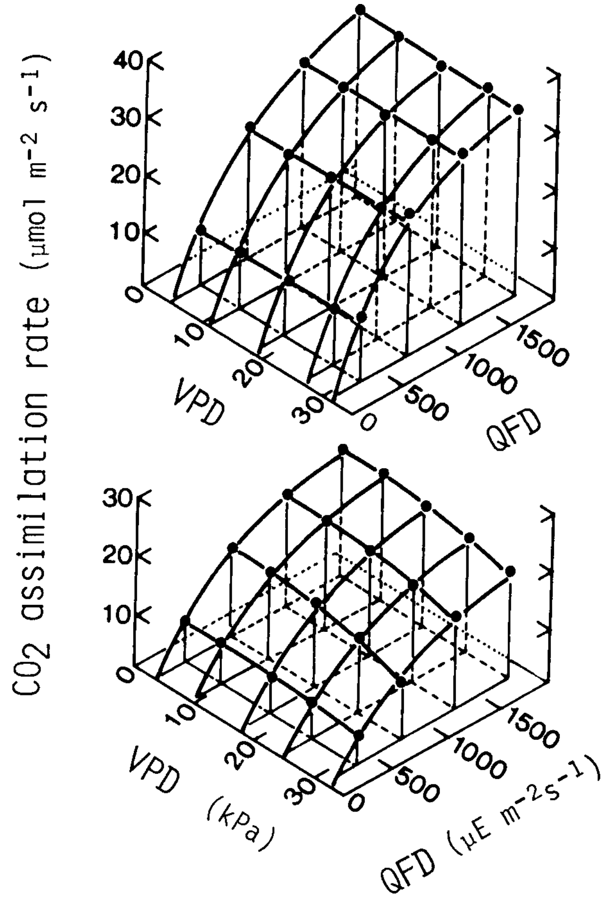

Fig. 2. Effects of vapour pressure difference (VPD) and quantum flux density (QFD) on CO, assimilation rate in C_4 species (*P. maximum* var. Maximum, upper) and C_3 species (0. *sativa* L. cv. Norin No. 18, lower).

leaf conductance. In the C_4 species, however, leaf conductance was remained almost constant with change in VPD. The diagram illustrates the fact that stomata of the C_3 species was more sensitive to VPD than that of the C_4 species under constant irradiances. In addition, a pronounced influences of irradiance on leaf conductance can be seen in the C_3 species as compared with the C_4 species.

Fig. 2 shows the responses of CO, assimilation rate to VPD and irradiance. A steady decline in CO, assimilaiton rate with increasing VPD was observed in the C_3 species at higher irradiances, but that of the C_4 species did not vary with change in VPD. At a given VPD, the responses of CO, assimilation rate to irradiance exhibited almost similar patterns in both C_3 and C_4 species. The maximum rates of CO_2 assimilation obtained at high irradiance and low VPD were 30 and 40 μmol m^{-2}s^{-1} for the C_3 and C_4 species, respectively.

Fig. 3 shows the effects of VPD and irradiance on water use efficiency, a ratio of CO, assimilation rate to transpiration rate per unit leaf area. The most notable difference between the two species is that the water use efficiency surface slope of the three-dimensional graph is more steepy in the C_4 species than in the C_3 species. At a given VPD, both species were able to maintain a nearly constant water use efficiency at irradiance exceeding 200 μE m^{-2}s^{-1}. Absolute water use efficiency of the C_4 species at any given irradiances was commonly higher than that of the C_3 species. This was probably due to the higher CO, assimilation rate and lower transpiration rate of the C_4

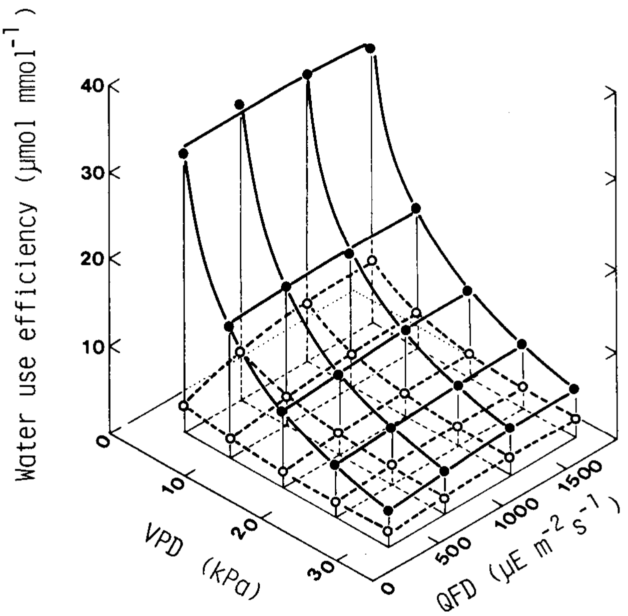

Fig. 3. Effects of vapour pressure difference (VPD) and quantum flux density (QFD) on water use efficiency for leaves of grass species. Solid and open circles denote the C_4 (*P. maximum* var, Maximum) and C_3 (*O. sativa* L. cv. Norin No. 18) species, respectively.

species. These figures (Figs. l-3) are a representative of the typical responses of CO, assimilation rate, leaf conductance and water use efficiency to the convined conditions of VPD and irradiance among the C_3 and C_4 grass species.

Table 1 shows the responses of these parameters to change in VPD under constant quantum flux density (2000 $\mu E\,m^{-2}s^{-1}$). In all species grown outdoors, there were decreases in CO, assimilation rate, leaf conductance and water use efficiency when VPD was increased from 14 to 28 kPa. The averaged decreases in CO, assimilation rate, leaf conductance and water use efficiency were 3.76 $\mu mol\,m^{-2}s^{-1}$, 61 mmol $m^{-2}s^{-1}$ and 6.1 μmol CO, mmolH_2O^{-1} for the C_4 species and 10 $\mu mol\,m^{-2}s^{-1}$, 160 mmol $m^{-2}s^{-1}$ and 2.0 μmol CO, mmolH_2O^{-1} for the C_3 species, respectively. Transpiration rates of the C_4 species were increased as the evaporative demands around the leaf were

Table 1. CO, assimilation rate (A), transpiration rate (E), leaf conductance (gl) and water use efficiency (WUE) at 28 kPa (high) and 14 kPa (low) leaf-to-air vapour pressure differrence, and stomatal frequncy (Sf) and length of the guard cells (Lg) on the adaxial (ad) and abaxial (ab) surfaces for leaves of C_3 and C_4 grass species. Measurements of leaf gas exchange were made at 30°C of leaf tempemperature and 2000 $\mu E\,m^{-2}s^{-1}$ of quantum flux density.

	A $\mu mol\,m^{-2}\,s^{-1}$		E mmol $m^{-2}\,s^{-1}$		gl mmol $m^{-2}\,s^{-2}$		WUE $\mu mol\,mmol^{-1}$		Sf No. mm^{-2}		Lg μm	
	low	high	low	high	low	high	low	high	ad	ab	ad	ab
C_3 species												
Arundo Donax	28.56	18.11	5.11	4.88	456.X	176.4	5.6	3.7	217	311	36.4	39.0
Hymenachne indica	19.41	10.97	3.76	2.67	267.6	93.9	5.1	4.1	119	98	45.3	49.0
Oryza sativa L. cv. Nihonbare	28.82	23.42	7.52	i.96	648.6	311.6	3.8	2.9	444	531	21.5	23.2
cv. Norin No. 21	17.99	13.84	3.12	3.36	235.5	122.8	5.8	4.1	398	470	22.7	20.8
cv. Nagakurabozu	20.83	13.41	3.76	3.67	283.5	130.2	5.5	3.7	447	516	17.4	18.9
Phalaris arundinacea	23.31	11.78	4.20	3.50	331.6	126.2	5.6	3.4	117	121	34.7	33.8
Mean and standard deviation	23.16 ±4.23	15.26 ±4.29	4.58 ±1.44	4.34 il.75	370.6 ±143.0	160.2 ±71.9	5.2 ±0.7	3.7 ±0.4	290 ±144	341 ±179	*29.i* ±9.8	30.8 ±10.9
C_4 species												
Arundinella hirta	*25.40*	*20.08*	*2.44*	*3.07*	*178.7*	111.1	10.4	6.5	53	81	46.7	47.3
Brachiaria brazantha	36.53	34.37	2.78	3.88	204.1	138.8	13.2	8.9	146	119	36.4	41.1
Cenchrus ciliaris	3i.36	35.99	3.19	4.27	215.X	147.4	11.7	8.4	111	141	37.0	37.8
Eleusine Coracana	28.23	22.28	2.12	2.63	140.4	90.7	13.3	8.5	136	72	33.1	38.3
Eragrostis ferruginea	24.99	23.68	2.12	2.61	147.5	92.8	11.8	9.1	186	114	25.8	30.8
Hyparrhenia rufa	40.69	37.06	3.06	3.92	224.9	139.9	13.3	9.5	50	16X	38.6	36.7
Panicum antidotale	35.13	31.29	2.53	3.86	178.4	140.7	13.9	8.1	145	159	28.5	28.4
P. coloratum var. kabulabula	30.81	25.35	2.06	3.02	147.6	103.9	15.0	8.4	144	120	28.9	33.3
var. makariense	38.14	37.51	2.66	3.19	197.4	117.3	14.3	11.8	121	103	31.0	37.6
P. dichotomiflorum	20.48	20.37	3.00	3.26	200.4	110.5	6.8	6.2	130	110	33.1	36.7
Paspalum dilatum	38.10	37.50	3.74	5.97	245.8	205.0	10.2	6.3	179	73	30.0	30.0
Setaria italica	38.75	30.43	2.93	3.67	21i.i	134.3	13.2	8.3	177	179	26.3	28.7
Sorghum bicolor	37.74	34.68	2.85	3.93	203.6	144.0	13.2	8.8	102	145	35.9	38.4
S. sudanese	40.30	37.78	3.35	5.68	252.8	216.0	12.0	6.7	77	127	38.9	39.9
hlean and standard deviation	33.76 ±6.29	30.60 ±6.60	2.77 ±0.47	3.78 ±0.97	196.8 ±33.7	135.2 ±35.8	12.3 i-2.0	8.3 ±1.4	126 ±41	122 ±33	33.6 ±5.6	36.1 ±5.1

increased, while those of the C_3 species were inversely decreased. CO, assimilation rate and water use efficiency were greater in the C_4 species than in the C_3 species irrespective of VPD levels.

The microscopic observation on the same leaf surfaces used for the gas exchange measurements confirmed that stomatal frequency of the C_3 species were greater than that of the C_4 species (Table 1). Smaller differences in stomatal frequency between adaxial and abaxial surfaces could be seen in the C_3 species, but not in the C_4 species. Among the C_3 species, in particular, A. *donax* and rice plants exhibited a greater stomatal frequency on their leaf surfaces. On the other hand, the length of the guard cells of these plants were smaller than those of the other C_3 and C_4 species.

DISCUSSION

Plants that have the C_4 photosynthetic pathway differ greately from C_3 plants in their physiological, biocemical, morphological, ultrastructural and ecological characteristics and their isotope discrimination value (Edwards and Walker, 1983). From the integration of these characteristics, it can be tentatively assumed that C_4 species derived from C_3 species in order to adapt themselves to relatively dry season and warmer region in the world (Black, 1971). In fact, many experimental studies have supported the assumption (Black, 1973 ; Agata *et al., 1985).* Ecological distribution of plant species is strongly governed by their physiological properties. But the basic information in regard to the limitation to the distribution have not been well-documented.

Since air humidity and temperature are strongly correlated with each other, it can be expected that C_4 species usually occurs in such habitats mentioned above and responses to humidity in different manners as compared with C_3 species. Morison and Gifford (1983) showed that the sensitivity of stomatal conductance to VPD was not different between two C_3 and two C_4 grass species, but it was linearly proportional to the magnitude of stomatal conductance. The results presented here, however, revealed that sensitivity of leaf conductance to VPD was greater in the C_3 species than in the C_4 species (Fig. 1). The percentages of the reduction in leaf conductance were about 56.8 % and 31.3 % for the C_3 and C_4 species, respectively, as VPD increased from 14 to 28 kPa (Table 1). Consequently, the reduction percent of CO, assimilation rate was 35.1% in the C_3 species whereas only 9.4 % in the C_4 species. The discrepancy between our results and Morison and Giff ord's is probably ascribed to the differences in growing and measuring conditions. Begg and Turner (1976) and Ludlow (1976) showed that stomatal sensitivity to the environmental variables depended largely on growing conditions, that is, stomata of plants grown under natural conditions was more sensitive than that of plants grown in greenhouse or growth cabinet. The species used in this study were all grown outdoors, therefore, it can be reasonably expected that the results presented here were almost similar to the responses obtained under natural conditions. Next, when VPD is zero, then transpiration rate would be zero. But the transpiration rates, extrapolated from the figure they presented (Morison and Gifford, 1983), do not indicate zero value at zero VPD. Probably the VPD were underestimated. This argument is additionaly supported by the fact that at the lower range of VPD their stomatal conductances were increased drastically with decreasing VPD.

Fig. 4 shows the relationship between CO, assimilation rate and leaf conductance in C_3 and C_4 species at both VPD levels (data obtained from Table 1). It is apparent that in both species there is a close correlation between them, indicating that the CO, uptake is strongly regulated by stomatal aperture. However, the response curve of the C_3 species saturates at about 400 mmol $m^{-2}s^{-1}$ of leaf conductance, and no further increase in CO, assimilation rate is detected although the stomata opens more. On the other hand, in case of the C_4 species it can further increase with increasing leaf conductance due to the lack of a saturation point in the CO, assimilation rate versus leaf conductance curve. At a given leaf conductance (e. g. 200 mmol $m^{-2}s^{-1}$), the rate of CO_2 asimilation of the C_4 species was Z-fold of that for the C_3 species. This is probably the reason why the existence of the C_4-dicarboxylic acid cycle, that is, the affinity for CO, of PEP-case which is an enzyme trapping CO_2 first in the mesophyll cells in C_4 species is higher than that of RuBP-case in C_3 species (Edwards and Walker, 1983). As a result, the C_4 species could attained the highest water use efficiency under such severe conditions.

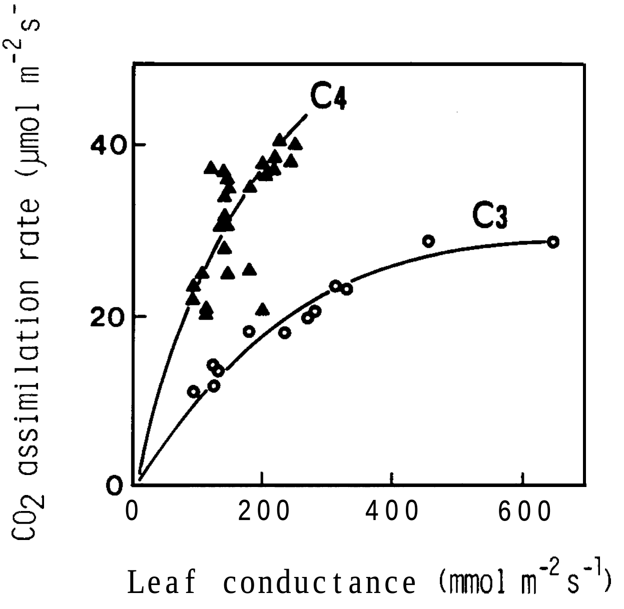

Fig. 4. Relationship between CO, assimilation rate and leaf conductance in grass species. Data obtained from Table 1.

When leaves are exposed to dry air the C_3 species showed rapid stomatal response as compared with the C_4 species. The stomatal responses to VPD in C_3 species seem to be a feedforward rather than negative feedback. Farquhar (1978) reported that stomatal response to VPD could be divided into examples of feedback and feedforward from the diagram of relationship between transpiration rate and VPD. Feedforward occurs when transpiration rate decline with increasing evaporative demand and accompanies by the presence of a peak rate of transpiration. In contrast, it is classified as feedback that transpiration rate linearly increases and never saturates with increasing VPD. According to the Farquhar's models, stomatal responses of the C_3 and C_4 species seem to be feedforward and feedback, respectively.

The reasons for exhibiting feedforward response in the stomata of C_3 species are not known. Possibly, to some extent, it may be explained by the differences in stomatal frequency, namely C_3 species have great amount of stomata on leaf surfaces in comparison with C_4 species. Feedforward hypothesis has been explained by direct cuticular water loss from guard and subsidiary cells (i. e. peristomatal transpiration) (Seybold, 1961/62; Lange et al., 1971). Increased stomatal frequency causes the enhancement of the presence of highly permeable regions in the cuticle (Schnherr and Bukovac, 1970). Consequenty, the C_3 species with a great number of stomata enable their stomata to response directly to VPD by means of peristomatal transpiration which is losses of some water from the leaf without passing through stomata.

In addition, presence of vein and bundle sheath extention and non-Kranz leaf anatomy may be correlated with the direct response to VPD. However, further investigation with more species are needed before definitive statements could be made about this phenomenon.

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