Plant Physiol. (1990) 92, 608-614
0032-0889/90/92/0608/07/$01.00/0

Received for publication May 16, 1989
and in revised form September 29, 1989

Effects of Water Vapor Pressure Deficit on Photochemical and Fluorescence Yields in Tobacco Leaf Tissue

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ABSTRACT

The relationship between photochemical quantum yield (Φ_s) and fluorescence yield have been investigated in leaf tissue from *Nicotiana tabacum* using CO_2 exchange and a modulated fluorescence measuring system. The quantum yield of CO_2 fixation at 1.6% (v/v) O_2 and limiting irradiance was reduced 20% by increasing the mean H_2O vapor pressure deficit (VPD) from 9.2 to 18.6 mbars. As [CO_2] and irradiance were varied, the intrinsic quantum yield of open photosystem II units (Φ_s/q_Q where q_Q is the photochemical fluorescence quenching coefficient) declined linearly with the degree of nonphotochemical fluorescence quenching. The slope and *y*-intercept values for this function were significantly reduced when the mean VPD was 18.4 millibars relative to 8.9 millibars. Susceptibility of the leaf tissue to photoinhibition was unaffected by VPD. Elevated O_2 concentrations (20.5% v/v) reduced the intrinsic quantum yield of net CO_2 uptake due to the occurrence of O_2-reducing processes. However, the relative effect of high VPD compared to low VPD on intrinsic quantum yield was not dependent on the O_2 level. This suggests that the Mehler reaction does not mediate the response of quantum yield to elevated VPD. The results are discussed with regard to the possible role of transpiration stress in regulating dissipation of excitation by electron transport pathways other than noncyclic electron flow supporting reduction of CO_2 and/or O_2.

Measurements of the quantum yield of photosynthesis at limiting irradiance levels in leaves and chloroplasts have affirmed the inherently high efficiency of light utilization under ideal conditions assuming applicability of the well-known *Z*-scheme to light-driven electron transport. Such experiments are normally carried out at low irradiance to assure that PSII electron acceptors are oxidized, *i.e.* PSII traps in the 'open' state. As the irradiance is progressively increased, a decline in quantum efficiency is commonly observed. This is due, in part, to closure of PSII centers as the plastoquinone pool becomes reduced resulting in higher probabilities of dissipation of radiant energy as heat or fluorescence (3, 6, 9, 18). Conditions of irradiance and availability of terminal electron acceptors during steady state photosynthesis are important factors influencing the proportion of PSII centers in the open state and capable of photochemistry.

A growing body of evidence indicates that the quantum efficiency of open PSII centers is regulated by dissipative processes which result in quenching of excitation in the antennae pigment complex and/or the PSII reaction center at the expense of photochemistry. This ensures that production of NADPH and ATP by the light reactions is matched to the prevailing capacity of the Calvin cycle to utilize these substrates during CO_2 fixation (6, 8, 21, 24).

Simultaneous application of pulse modulated fluorescence and gas exchange methods to photosynthetic systems is helping to resolve changes in radiant energy utilization under diverse environmental conditions (22). Because of the existence of multiple mechanisms for fluorescence quenching in PSII, relationships between changes in fluorescence and photochemical yields have been difficult to interpret. The pulse-modulated technique permits separation and quantitation of fluorescence quenching associated with the redox state of the first stable electron acceptor in PSII, Q_A (*i.e.* photochemical quenching). A second collective source of quenching (nonphotochemical) is caused by diversion of excitation from PSII to PSI (state transitions) and conversion of quanta to heat in the antennae complex and possibly at the PSII reaction center (12, 19). Dissipation of light energy as heat is associated with the magnitude of the thylakoid pH gradient and photoinhibition (4, 5, 9, 11).

Several previous reports have noted an inverse relationship between the quantum yield of photochemistry for open PSII centers versus the degree of nonphotochemical quenching as expressed as the coefficient q_{NP}[1] (9, 18, 21, 24). In this paper, I extend studies of the relationship between q_{NP} and photochemical quantum yield of open PSII centers to leaf tissue subjected to mild water stress created by a high transpiration rate. This subject has ecological relevance to plant water relations and photosynthesis as well as importance to an understanding of radiant energy utilization in leaves.

MATERIALS AND METHODS

Plant Material

Nicotiana tabacum var Havana Seed was grown in pots in a greenhouse and leaf discs were prepared as described previ-

[1] Abbreviations: q_{NP}, nonphotochemical fluorescence quenching coefficient; A, CO_2 assimilation rate; g_{H_2O} total gas phase conductance to H_2O; VPD, vapor pressure deficit; F, steady state fluorescence yield; F_o, steady state fluorescence yield observed after prolonged exposure to darkness; F_o', fluorescence yield observed during brief (2–4 s) interruption of actinic illumination; F_s, fluorescence yield observed during a saturating flash superimposed upon actinic illumination; F_m, maximum fluorescence yield in the absence of ΔpH-dependent quenching; F_{max}, maximum fluorescence yield observed when all quenching mechanisms are relaxed (fully dark-adapted leaf); q_Q, photochemical fluorescence quenching coefficient; q_R, nonphotochemical quenching coefficient when ΔpH-dependent mechanism is relaxed; Φ_s, quantum yield of net CO_2 fixation (mol CO_2:mol incident photons); $\Phi_p = \Phi_s/q_Q$ = intrinsic quantum yield of CO_2 fixation; R, correlation coefficient ($P < 0.01$).

ously (17). The plants were watered daily and cultured weekly with a solution of 20-20-20 (N-P-K) fertilizer and Hoagland micronutrients. The experiments were conducted during the months of February and March of 1989.

Gas Exchange

Transpiration and CO_2 assimilation rates were measured using an open, flow-through system and infrared gas analysis (13, 17). Distilled H_2O was supplied to the cut edges of a 5 cm diameter leaf disc mounted in a Leaf Section Chamber (Analytical Development Co., Hoddesdon, U.K.). The edges of the leaf disc were sealed off from the central illuminated area (10 cm^2) with soft rubber O-rings and silicone grease. The leaf disc divided the chamber volume into two compartments. The gas stream (total flow rate = 2.0 L min^{-1}) was divided equally just upstream from the chamber, each compartment was flushed independently, and then the gas streams were recombined.

The H_2O vapor concentration in the flushing gas was set at 10 or 20 mbars below the saturation vapor pressure at 25°C (leaf temperature) by varying the temperature of a condenser through which the gas stream (saturated with H_2O) was passed. These conditions correspond to RH levels for the flushing gas of 68 and 36%, respectively. The gas stream was then split with one portion (reference stream) flushing the reference cell of the H_2O IRGA and the sample cell of the CO_2 IRGA. The remainder of the flushing gas (sample stream) passed through a mass flowmeter, the leaf chamber, the reference cell of the CO_2 IRGA, and the sample cell of the H_2O IRGA. This arrangement resulted in upscale instrumental responses to transpiration and CO_2 assimilation by the respective IRGAs operating in the differential mode. A cartridge containing the desiccant Drierite ($CaSO_4$) was located just upstream from the CO_2 IRGA in the reference stream. This was to eliminate any possible effects of fluctuating H_2O vapor levels in the reference stream on the response of the CO_2 IRGA to $\Delta[CO_2]$. A system of solenoid valves permitted bypassing of the leaf chamber by the sample stream to obtain instrumental null responses. In experiments in which the leaf disc was replaced by a droplet of H_2O in the chamber the CO_2 IRGA showed a slight response to the increase in the $[H_2O]$ of the sample stream due to simulated transpiration ($\Delta[H_2O]$:$\Delta[CO_2]$ relative IRGA response about 3000). Both this cross-sensitivity to $\Delta[H_2O]$ and the dilution of CO_2 due to transpiration (13) have been compensated for in the CO_2 assimilation rates reported. Illumination was supplied to the adaxial surface of the leaf disc. Leaf temperature was measured within 0.1°C by a thermistor in contact with the abaxial surface of the leaf disc.

Fluorescence Measurements

The PAM 101 Fluorescence Measuring System (H. Walz, Effeltrich, F.R.G.) was employed as described previously (17) to measure variable fluorescence yield from the adaxial surface of the leaf disc. Figure 1 illustrates the experimental protocol employed and defines quenching coefficients and other variables used herein. Values for q_Q and q_{NP} were calculated from changes in modulated fluorescence yield associated with three successive pulses of saturating while light

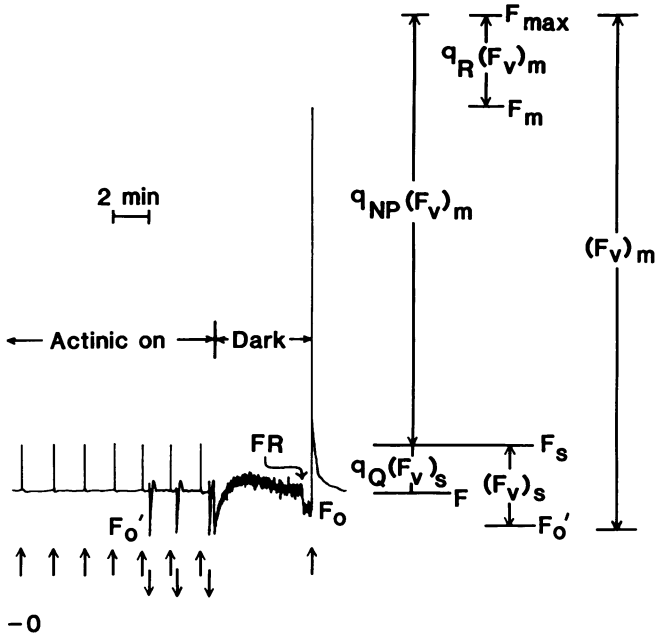

Figure 1. Definition of quenching coefficients and fluorescence yield changes for a typical experiment performed with tobacco leaf tissue (actinic irradiance = 845 μmol photons m^{-2} s^{-1}, 1.6% O_2 v/v, 349 μbars CO_2, 25°C). Pulses of saturating white light were applied at 100 s intervals (↑) during actinic illumination. The steady state basal fluorescence yield (F_o') was estimated by recording the response during a 2 to 4 s dark interval between successive saturating pulses (↓). The actinic illumination and saturating pulses were then discontinued for 5 min to allow the rapidly reversible component of nonphotochemical quenching to relax. Application of a weak FR background illumination frequently lowered the F_o level presumably by causing photooxidation of the intersystem electron transport chain (24). A saturating pulse was then applied to the darkened sample to obtain the F_m fluorescence yield. Fluorometer measuring beam modulation frequencies were 100 kHz and 1.6 kHz during actinic illumination and darkness, respectively. Other details of the procedure are described in "Materials and Methods."

(7500 μmol photons m^{-2} s^{-1} for 0.7 s). The sample was then darkened for 5 min during which time nonphotochemical quenching relaxed considerably. Another saturating pulse of white light was applied, and the F_o and F_m levels were recorded. The ratio F_v/F_m was calculated as $(F_m-F_o)/F_m$ (4, 5).

RESULTS

Effects of VPD on Net Photosynthesis and Fluorescence Quenching

Figure 2 shows changes in net CO_2 assimilation as irradiance was progressively increased at a mean external $[CO_2]$ of 335 (SD = 16) μbars and 17 mbars O_2 (1.6% v/v). The mean vapor pressure deficit was the vapor pressure at leaf temperature minus the mean vapor pressure of the chamber gas (computed as the average vapor pressure of the gas entering and that exiting the chamber). The mean VPD was either 9.0 (SD = 0.4) or 18.1 (SD = 0.7) mbars. The initial slope of the A *versus* irradiance curves and the light saturated rates were both lowered by raising the mean VPD from 9.0 to 18.1 mbars. In contrast no significant effect of VPD on q_Q or q_{NP}

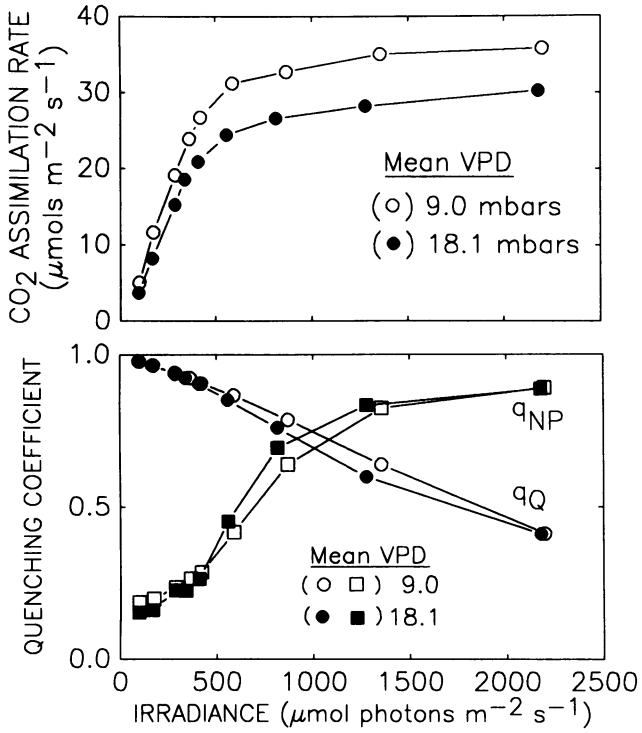

Figure 2. Effect of VPD on the light response of net CO_2 assimilation (top panel) and of q_Q and q_{NP} (bottom panel) at 1.6% O_2 (v/v) for tobacco leaf tissue. The mean chamber gas CO_2 concentrations were 335 (SD = 22) and 336 (SD = 8) μbars at mean VPD levels of 9.0 (SD = 0.4) and 18.1 (SD = 0.7) mbars, respectively. Each point is a mean of duplicate determinations performed with separate leaves.

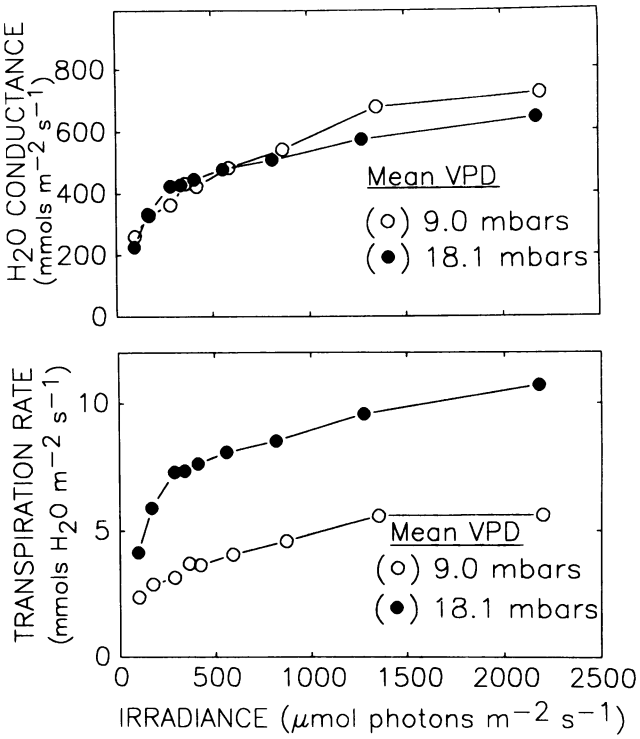

Figure 3. Mean values for total gas phase conductance to H_2O (g_{H_2O}) (top panel) and transpiration rates (bottom panel) for the data of Figure 2.

was observed. For these same experiments increasing the VPD from 9.0 to 18.1 mbars doubled the transpiration rate (Fig. 3, bottom). The increase in mean VPD did not cause a change in total gas phase conductance to H_2O (Fig. 3, top). Note that gradients of H_2O vapor pressure averaging 2 to 4 mbars were created in the unstirred assimilation chamber (see "Materials and Methods"). Also, the gas inlet and outlet ports of the Leaf Section Chamber are distributed along the circular margin of the internal cavity insuring uniform gas flow over the leaf.

A decrease in the ratio F_v/F_m, as measured after a suitable dark period to remove the effects of ΔpH-dependent fluorescence quenching, has been employed as a measure of photoinhibitory effects on the photosynthetic apparatus (4, 5). For the experiments shown in Figure 2, the mean F_v/F_m declined from a level of 0.80 to 0.69 over the range of irradiances tested and, again, was independent of VPD. The mean F_v/F_m for dark-adapted samples was 0.84.

The effect of mean VPD on limiting quantum yield (Φ_s) was investigated further by measuring the slope of A *versus* irradiance curves at low photon fluxes where this relationship is linear (Table I). Note that the term 'limiting quantum yield' as used here applies to low irradiance conditions, whereas 'quantum yield' implies no restrictions on the irradiance employed. A 20% inhibition of limiting Φ_s was noted at a VPD of 18.9 mbars relative to 9.2 mbars. Again, no effect of VPD on F_o, F_m, F_v/F_m, or dark respiration was observed.

The measurements of F_o in these experiments were performed without a FR background illumination. A prior report (18) and current efforts in this laboratory indicate that FR illumination does not appreciably affect the steady state fluorescence measured during a brief interruption of actinic illumination (F_o'). Also, the levels of F_o and F_o' are similar at low irradiances. Thus, the F_o values in Table I were measured during brief dark intervals under steady conditions of photosynthesis at the lowest irradiance employed (80 μmol photons m^{-2} s^{-1}). Lack of an FR background illumination is presumed to cause a slight underestimation of the F_v/F_m values reported above for the experiments of Figure 2.

Effects of Irradiance, VPD, and CO_2 Concentration on the Relationship between Intrinsic Quantum Yield and Nonphotochemical Quenching

Weis and Berry (24) have defined intrinsic PSII quantum yield (Φ_p) as the ratio Φ_s/q_Q. This permits estimation of the photochemical yield of PSII if all of the centers were in the open state. These authors also reported that Φ_p and q_{NP} were inversely and linearly related regardless of whether irradiance or [CO_2] was varied. This observation is confirmed with tobacco (Fig. 4). A heretofore unreported property of this response is the sensitivity to mean VPD. The slope and *y*-intercept values for the Φ_p *versus* q_{NP} relationship are significantly lower by 28.0% and 20.9%, respectively, at a mean VPD of 18.4 (SD = 0.4) mbars as compared to 8.9 (SD = 0.1) mbars. As q_{NP} approaches 1.0, however, the lines meet at a Φ_p of about 0.03 mols CO_2: mol photons. Clearly, the effect

Table I. *Effect of Change in VPD on Dark Respiration, Photochemical Quantum Yield, and Fluorescence Yield in Tobacco Leaf Tissue*

The $[O_2]$ was 1.6% (v/v) and the leaf temperature was 25°C. The chamber $[CO_2]$ varied from 330 to 600 μbars among the experiments shown. Two to four measurements of net $[CO_2]$ uptake were performed at irradiances ranging from 80 to 300 μmol photons m^{-2} s^{-2} which constituted the linear response range. Limiting quantum yield was estimated as the slope of the A *versus* irradiance function using linear regression. The dark respiration rate is the extrapolated value of A at zero irradiance based on the linear regression equation. Fluorescence yield values (F_o and F_m, see Fig. 1) are normalized such that at a VPD of 18.9 mbars F_m = 1.000. Values in parentheses are standard errors.

VPD	Dark Respiration	Limiting Quantum Yield[a]	q_O	F_o	F_m	F_v/F_m
	μmol CO_2 m^{-2} s^{-1}			arbitrary units		
9.2	2.2	0.0753	0.961	0.199	0.974	0.795
(0.3)	(0.5)	(0.003)	(0.001)	(0.007)	(0.045)	(0.004)
18.9	2.3	0.0602	0.960	0.194	1.000	0.807
(0.5)	(0.4)	(0.002)	(0.003)	(0.008)	(0.023)	(0.005)

[a] mol CO_2: mol photons.

of mean VPD on Φ_p diminishes as q_{NP} increases with irradiance.

At all of the CO_2 concentrations tested, irradiance was the main determinant of total gas phase conductance to H_2O (g_{H_2O}). Three-way analysis of variance of the main effects of irradiance, mean VPD, and chamber gas $[CO_2]$ (latter includes biological variability among leaves) was performed on the associated g_{H_2O} values determined in the experiments of Figure 4. Partitioning of the sums of squares among these effects indicated that irradiance accounted for 74% of the variation in g_{H_2O} while $[CO_2]$ and VPD accounted for only 7% and 5%, respectively.

Vapor Pressure Deficit and Photoinhibition

Nonphotochemical quenching of variable fluorescence may be resolved into components based on relaxation times of quenching of F_m in darkness (5, 9). Energy-dependent quenching which is associated with the magnitude of the thylakoid pH gradient (9) is assumed to decline to minimal levels within minutes of darkening. The remaining slowly reversible component (photoinhibition) is considered to arise from enhanced thermal dissipation in the antennae pigment complex (5). This component would also include any phosphorylation-dependent PSII⟶PSI excitation transfer (state transitions), but this is probably of quantitative importance only at low irradiance levels (9). Following steady state CO_2 exchange and fluorescence yield measurements the change in fluorescence yield during a saturating flash of white light was measured after 300 s of darkness (see Fig. 1). The F_m level was essentially unchanged after an additional 100 s of darkness. The quenching coefficient q_R provides a measure of the extent of this slowly reversible component (Fig. 1). Comparisons of q_R with total nonphotochemical quenching (q_{NP}) for all of the experiments of Figure 4 is presented in Figure 5. The relative magnitude of q_R increases rapidly as q_{NP} rises above 0.7, but the increase is similar for VPD levels of 8.9 and 18.4 mbars. Also, no consistent effect of chamber $[CO_2]$ is apparent in these experiments and the residual variability in q_R most likely reflects inherent differences in susceptibility to photoinhibition among the leaf samples employed.

Interactive Effects of Elevated $[O_2]$ and Vapor Pressure Deficit on Intrinsic Quantum Yield

When the $[O_2]$ in the atmosphere around the test leaf was increased to 217 mbars (20.6% v/v) at near atmospheric $[CO_2]$, a substantial decline in Φ_p was observed relative to low $[O_2]$ (Fig. 6). This was caused by activation of O_2-reducing processes such as photorespiration. In an earlier report (17), I defined a parameter, P_{diss}, as the proportion of total noncyclic photosynthetic electron transport supporting dissipative, O_2-dependent processes. At any constant value for q_{NP}, $P_{diss} = (\Phi_p'-\Phi_p)/\Phi_p'$ where Φ_p' is the predicted intrinsic quantum yield at low $[O_2]$ (dashed lines, Fig. 6). Values of Φ_p obtained from light response curves at high $[O_2]$ formed a straight line when plotted *versus* associated values of q_{NP}. No observable trends in P_{diss} with increasing q_{NP} were apparent (not shown). The mean values of P_{diss} for the two VPD levels are shown in Figure 6 and do not differ substantially. This indicates that the effect of elevated VPD was to reduce quantum yield to similar extents regardless of the level of O_2. Thus, O_2 probably did not influence the response of the photosynthetic apparatus to transpiration stress.

DISCUSSION

Since the decreased RH in these studies increased the transpiration rate with little effect on total gas phase conductance, I will assume that the transpiration rate mediates the observed decline in the quantum yield of CO_2 fixation. Numerous studies have been concerned with the nonstomatal inhibition of photosynthesis in leaves in response to drought created by low soil moisture. Soil moisture deficits generally lead to a decrease in the water potential of the leaf mesophyll cells. Sharkey (20) concluded that rapid loss of water from leaves could likewise bring about a decline in water potential resulting in diminished photosynthetic capacity at the cellular level.

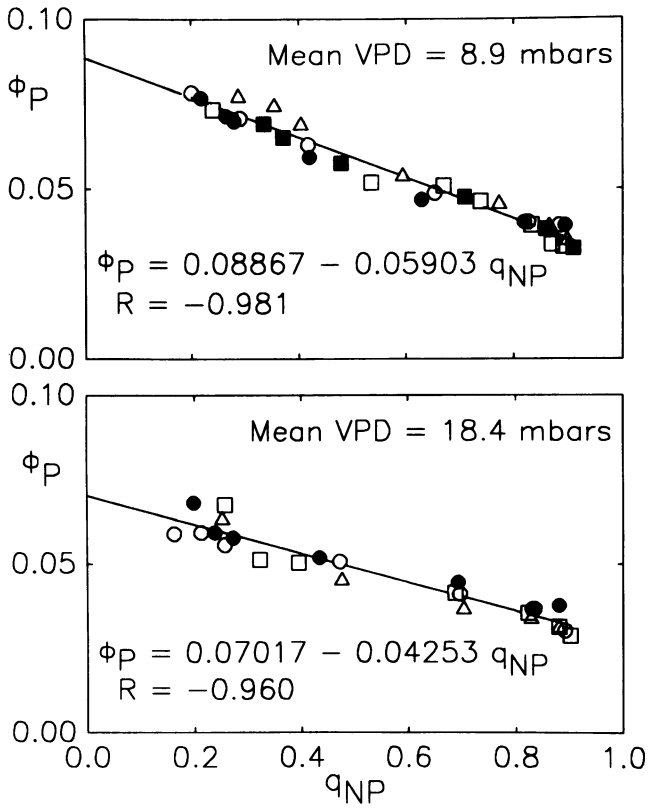

Figure 4. Relationship between intrinsic quantum yield (Φ_p) and q_{NP} at two mean VPD levels for tobacco leaf tissue. The [O_2] was 1.6% (v/v) for all of the experiments. Irradiance was varied from 80 to a maximum of about 2200 μmol photons m^{-2} s^{-1} except at the lowest [CO_2] (150, SD = 4 μbars) where the maximum was 1275 μmol photons m^{-2} s^{-1} (top panel, □). Other chamber CO_2 levels (±SD) were (○), 315 ± 15; (●), 352 ± 10; (■), 457 ± 7; (△), 600 ± 15 μbars (top panel) and (□), 267 ± 7; (○), 335 ± 10; (●), 337 ± 5; (△), 508 ± 5 μbars (bottom panel). Each point is the result of a single determination of photochemical and fluorescence yields. The solid lines are linear regression fits (equations shown in panels) for the respective sets of data.

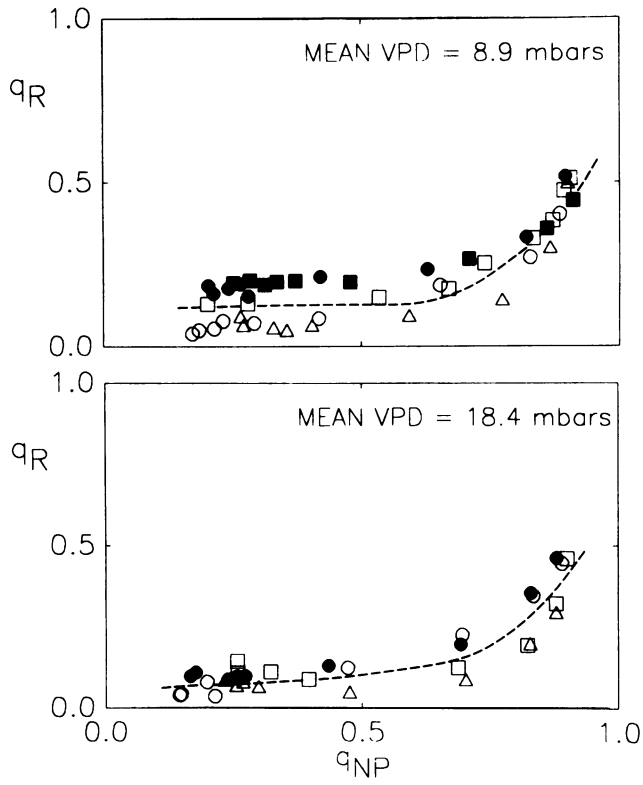

Figure 5. Relationship between q_R and q_{NP} for the data from Figure 4.

The exact cause of inhibition of photosynthesis in isolated chloroplasts and protoplasts subjected to decreased osmotic potential remains unclear but several mechanisms could be involved. Kaiser (10) suggested that increased intracellular solute concentrations in response to decreased protoplast volume resulted in inhibition of enzyme activities necessary for CO_2 fixation. Berkowitz and Gibbs (2) presented evidence for inhibition of Calvin cycle turnover in isolated chloroplasts due to stromal acidification during osmotic stress. Previous reports have described a decline in the limiting quantum yield of net photosynthesis following water stress (1, 14, 15, 20).

A primary benefit of simultaneous measurement of photochemical and fluorescence yield is that assessment of the efficiency of radiant energy utilization (as $\Phi_p = \Phi_s/q_Q$, see ref. 24) can be extended to saturating irradiances. Of special significance is how the relationship between Φ_p and q_{NP} is influenced by changes in VPD. Components of nonphotochemical quenching of fluorescence have been distinguished on the basis of the half-times necessary for their relaxation (5, 9). The ΔpH-dependent component relaxes with a half-time of <1 min while phosphorylation-dependent (state transitions) and reversible quenching in the antennae complex induced by excessive irradiance exhibit half-times for relaxation of about 5 and 30 min or longer, respectively. The quantitative relationships between the individual mechanisms of fluorescence quenching and Φ_p are not well understood at this time. One might suggest, therefore, that variations in the composition of nonphotochemical quenching of excitation in response to changing mean VPD may underlie the different dependencies of Φ_p on q_{NP} observed in Figure 4. This seems unlikely, however, since VPD did not influence the relationship between q_R and q_{NP} (Fig. 5).

Another means by which an increase in mean VPD might change the relationship between Φ_p and q_{NP} is via damage to the primary photochemistry of PSII. Low leaf water potentials have been reported to cause a decline in PSII electron transport activity in isolated chloroplasts from sunflower (14). The F_v/F_m appears to be quite sensitive to reaction center inactivation since it results in an increase in F_o with little effect on F_m (4, 5). Again, no effect of mean VPD on either F_o or F_v/F_m was apparent in these studies (Table I).

The decline in photochemical quantum efficiency of PSII appears, therefore, to occur by a mechanism which is not detectable by a change in fluorescence yield. Support for this conclusion comes from work with *Helianthus annus* and *Xanthium strumarium* plants subjected to water stress in

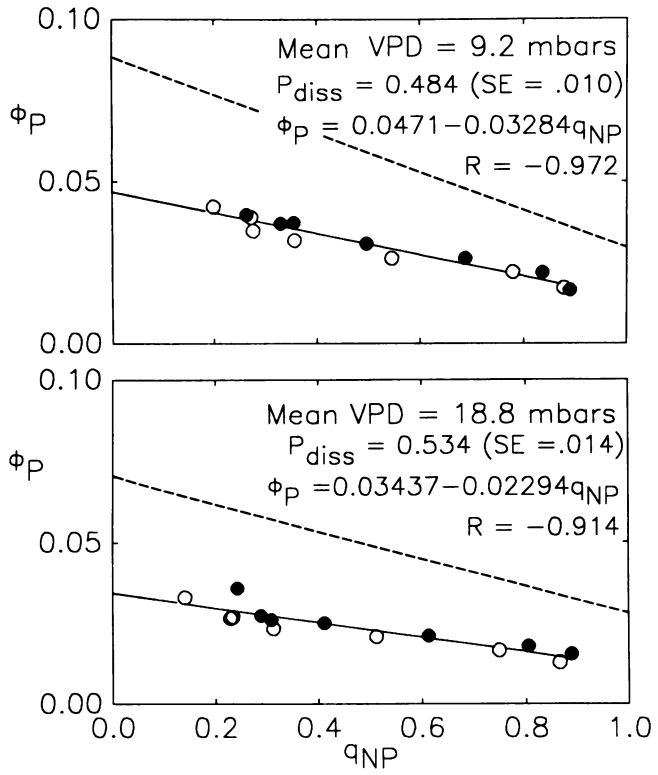

Figure 6. Relationship among mean VPD, Φ_p, and q_{NP} at an atmospheric $[O_2]$ of 20.6% (v/v). Irradiance was varied from 80 to about 2000 μmol photons m^{-2} s^{-1}. In the top panel the mean VPD was 9.2 (SD = 0.4) mbars and the CO_2 level was 364 (SD = 10) μbars. In the bottom panel the mean VPD was 18.8 (SD = 0.4) mbars and the CO_2 level was 358 (SD = 7) μbars. Shown are results of two independent experiments at each mean VPD. See text for discussion of P_{diss}. The solid lines are linear regression fits (equations shown in panels) for the respective sets of data. Dashed lines are the respective regression lines for the Φ_p *versus* q_{NP} relationship at 1.6% O_2 and corresponding VPD levels obtained from Figure 4.

which no effect on the F_v/F_m in leaves at 77°K was observed (1). Oxborough and Horton (16) reported that antimycin A nearly abolished energy-dependent fluorescence quenching in chloroplasts with no apparent effect on the ΔpH or Φ_p. They suggested that both the ΔpH and the redox state of a component of the cyclic electron transport system coordinately regulate energy-dependent quenching. A futile PSII electron transport cycle was postulated as an alternate mechanism of energy dissipation in the absence of nonphotochemical quenching of excitation. I suggest that activation of such a futile PSII cycle in response to transpiration stress could account for the results described herein. Replacement of noncyclic electron transport to CO_2 by Mehler-type processes involving PSI in response to increased VPD seems an unlikely explanation for the results of Figure 4. Elevated $[O_2]$, which would be expected to enhance the Mehler reaction (7), did not appreciably alter the relative response of the Φ_p *versus* q_{NP} relationship to increased VPD (Fig. 6).

A recent report (23) indicated that nonuniform stomatal closure can occur in leaves of certain species in response to treatment with abscisic acid. The possibility that such 'patchiness' in photosynthesis may in some way underlie the responses to increased VPD presented here must be considered. No direct observations of stomatal aperture were performed. The occurrence of sporadically closed stomates could lower Φ_s as measured here (Table I) since the intercellular $[CO_2]$ associated with such patches could be rate-limiting. Fluorescence yield measurements would then represent an average of any effects of spatial heterogeneity occurring within the field of illumination by the measuring beam (about 1.8 cm^2). An immediate effect of occurrence of such patches of closed stomates would have been a change in q_Q. The magnitude of q_Q has been shown to decline as the $[CO_2]$ is lowered in intact leaves (6, 18). No such independent effect of VPD on q_Q was observed (Table I; Fig. 2) arguing against a purely stomatal basis for the results presented.

These results indicate that transpiration rate is an important variable in the relationship between photochemical and fluorescence yields. The role of environmental conditions in regulating energy dissipating processes must be understood before fluorescence measurements may be developed into a rapid, reliable and convenient screening tool for superior photosynthesis and growth.

ACKNOWLEDGMENTS

I wish to thank Nancy Burns for skillful technical assistance and Israel Zelitch for helpful comments on the manuscript.

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