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Quantum Yields of Photosystem II and Photosynthesis in an Aurea Mutant of Tobacco (C_3) and an Oil Yellow Mutant of Maize (C_4) Which Have High Capacities for Photosynthesis Despite Low Chlorophyll Contents

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The quantum yields of O_2 evolution (ϕ_{O_2}), CO_2 fixation (ϕ_{CO_2}), and of photosystem II measured by fluorescence analysis (ϕ_{PSII}), were determined in a mutant of tobacco (C_3) and a mutant of maize (C_4) having large deficiencies in light harvesting chlorophyll, but having similar capacities for photosynthesis on a leaf area basis as the wild-type plants. The heterozygous dominant mutant of tobacco (aurea, Su/+) having 30% chlorophyll content of the wild-type, and of maize (oil yellow, Oy/+) having 60% chlorophyll content of the wild-type, maintain high leaf absorptances. The maximum ϕ_{O_2} on an absorptance basis, measured under limiting red light and saturating CO_2 were the same in the mutant versus wild-type plants. ϕ_{PSII} and ϕ_{CO_2} decreased in a similar manner with increasing light intensity, while the ratio of ϕ_{PSII}/ϕ_{CO_2} under varying light remained reasonably constant, in mutant versus wild-type seedlings. The results indicate that these C_3 and C_4 mutants which have high capacities for photosynthesis despite large deficiencies in chlorophyll content, maintain a high leaf absorptance, and a balanced utilization of absorbed quanta in photochemistry.

Key words: C_3 plants — C_4 plants — Fluorescence — Light — Photosystem II — Quantum yield.

Using modulated light to measure Chl *a* fluorescence emitted from PSII, it is possible to distinguish between the utilization of absorbed energy in photochemical versus non-photochemical processes and to determine ϕ_{PSII}, the quantum yield of PSII according to the model of Genty et al. (1989). By simultaneous determination of ϕ_{PSII} and the quantum yield of carbon assimilation (ϕ_{CO_2}), the efficiency of utilization of photochemically derived energy for photosynthesis can be analyzed under varying environmental conditions. Since ϕ_{CO_2} equals the rate of CO_2 fixation divided by the light absorbed by the leaf, and ϕ_{PSII} equals electrons derived from water oxidation per quanta absorbed by PSII, then

$$\frac{\phi_{PSII}}{\phi_{CO_2}} = \frac{I_L}{I_{PSII}} \cdot \frac{J_e}{A^*} \qquad \text{eqn 1}$$

According to this equation, the relationship between ϕ_{PSII}/ϕ_{CO_2} is dependent on the distribution of light absorption between the photosystems and the rate of noncyclic electron flow (J_e) per CO_2 fixed. In C_3 plants, there is an increase in the J_e/A^* ratio with increased partitioning of energy to photorespiration through changes in $[CO_2]$ or $[O_2]$ (Peterson 1989, Harbinson et al. 1990, Krall and Edwards 1990, Cornic and Briantais 1991, Krall and Edwards 1992) which causes an increase in the ϕ_{PSII}/ϕ_{CO2} ratio. In C_4 plants, the ϕ_{PSII}/ϕ_{CO2} ratio is relatively constant with varying $[CO_2]$, $[O_2]$, temperature and PPFD because photorespiration is minimal and CO_2 fixation appears to be closely linked to PSII activity (Genty et al. 1989, Krall and Edwards 1990, 1992, Oberhuber and Edwards 1993, Oberhuber et al.

Abbreviations: A, measured rate of CO_2 assimilation; A*, rate of CO_2 assimilation corrected for dark-type respiration (A+ R_d); F_m', yield of PSII chlorophyll *a* fluorescence due to a saturating flash of white light under steady-state photosynthesis; F_s, variable yield of fluorescence under steady-state photosynthesis; PPFD, photosynthetic photon flux density; I_L, PPFD absorbed by leaf; I_{PSII}, PPFD absorbed by PSII; PSII, photosystem II; J_e, rate of whole chain electron flow; R_d, rate of respiration in the dark; ϕ_{O_2}, quantum yield for oxygen evolution; ϕ_{CO_2}, quantum yield of CO_2 assimilation; ϕ_{PSII}, electrons transported via PSII per quantum absorbed by PSII.

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1993, Edwards and Baker 1993). Analysis of the relationship between ϕ_{CO_2} and ϕ_{PSII} can also be made with chlorophyll deficient mutants to determine whether such mutants have an imbalance in light absorption by PSI and PSII, as this would affect the I_L/I_{PSII} ratio. In the present study, we analyzed the relationship between the quantum yield of photosynthesis and that of photosystem II in a mutant (Su/+) of the C_3 plant tobacco and a mutant (Oy/+) of the C_4 plant maize. These mutants, despite having a large deficiency in light harvesting Chl, are remarkably efficient in utilization of solar energy for photosynthesis.

Materials and Methods

Plant material and growth conditions—Tobacco (*Nicotiana tabacum* L.) seeds were germinated in a 24 h continuous light chamber at 20–21°C. The wild-type and mutant plants were derived from a seed lot of a heterozygote cross of two Su/+ mutants. After germination, seedlings were transplanted into pots and placed in a growth chamber with a 12 h/12 h photoperiod at 30°C/18°C and a PPFD of 200–300 μmol quanta $m^{-2} s^{-1}$. Maize (*Zea mays* L.) was grown in a growth chamber under a 16 h/8 h photoperiod at a day/night temperature of 28°C/18°C under a PPFD of ca. 500 μmol quanta $m^{-2} s^{-1}$. The Oy/+ plants were grown from a seed lot from a cross of Oy/+. Wild-type maize plants used were the +/+ siblings from the heterozygote cross. The soil used in growing plants contained 55% peat, 35% pumice, 7.5% pumice sand, 2.5% medium washed sand, plus nutrients [3 g $liter^{-1}$ limestone ($CaCO_3$), 3.5 g $liter^{-1}$ polomite lime, 0.4 g $liter^{-1}$ KNO_3, 0.4 g $liter^{-1}$ $FeSO_4$, 0.5 g $liter^{-1}$ treble super phosphate ($CaPO_4$), 0.12 g $liter^{-1}$ sulfur, 0.04 g $liter^{-1}$ $MnSO_4$ and 0.1 g $liter^{-1}$ micronutrient].

CO_2 fixation and fluorescence measurements—Experiments were conducted in a growth chamber equipped for simultaneous measurements of CO_2 exchange and fluorescence as described in Krall and Edwards (1990). The leaf temperature (measured at the lower surface with a thermocouple) was maintained at 30°C. The second or third youngest leaf of either tobacco or maize was placed in a temperature-controlled cuvette and the enclosed leaf segment was illuminated by an overhead metal halide lamp. PPFD was varied by laying different amounts of cheesecloth over the sealed cuvette. Steady-state CO_2 uptake was measured with an Analytical Development Company (ADC) infrared gas analyzer (225-MK3). Gas flow was controlled by a Bingham Interspace Model BI-2 controller. This open system design was operated in the differential mode. Measurements were made under normal air (ca. 340 μbar CO_2 and 21% O_2) or under high CO_2 and low O_2 (ca. 700–1,000 μbar CO_2, 2% O_2). For measurements of photosynthesis, the CO_2 removed by the carbon assimilation was replaced from a 2,000 μbar CO_2 source so that the concentration around the leaf was kept constant. Calculations of gas exchange were made according to von Caemmerer and Farquhar (1981). Rates of respiration in the dark were measured after having plants in the dark for 30 to 60 min and prior to measurements of the photosynthetic light response curves which were conducted from low to high PPFD. The steady-state quantum yields of CO_2 assimilation (ϕ_{CO_2}) were calculated from the rate of CO_2 assimilation (A*) divided by the respective absorbed quanta.

Fluorescence measurements were made with a pulse amplitude modulation fluorometer (Walz Model 101, H. Walz, Effeltrich, Germany or Hansatech Model MFMS/2T, Kings Lynn, Norfolk, England). The fluorometer, including the fluorescence detector which is temperature sensitive, was set up in a growth chamber at room temperature. The probe was positioned above the cuvette at an angle so as not to interrupt the incident illumination. F_s is the steady-state fluorescence yield under a given environmental condition and F_m' is the fluorescence yield when a saturating pulse of white light is supplied to the leaf under these same environmental conditions. At steady state photosynthesis under a given condition, F_s was monitored continuously, and, for periodic determination of F_m', saturating pulses (800 ms duration) of white light (about 9,000 μmol quanta $m^{-2} s^{-1}$) were applied automatically at 300 s intervals. The leaf was allowed to equilibrate in terms of both carbon assimilation and fluorescence parameters at each PPFD before measurements were made (the average equilibration time at each PPFD was about 20 to 30 min). The quantum yield of PSII electron transport (ϕ_{PSII}) was calculated as $(F_m'-F_s)/F_m'$, following the method of Genty et al. (1989).

Oxygen exchange measurements—The Hansatech oxygen electrode apparatus (Hansatech Limited, Kings Lynn, Norfolk, U.K.) was utilized to measure the quantum yield of O_2 evolution under limiting light at 20°C in an atmosphere containing 1% CO_2 (Walker 1987). Actinic red light was supplied by a Hansatech LED unit (Model LS1).

Measurement of PPFD and pigment analysis—Chlorophyll content was measured using 80% acetone as a solvent (Arnon 1949). Measurement of PPFD from the light emitting diodes (LED) in O_2 exchange studies were made with a sensor (Skye Instruments) designed to fit over the transparent window of the Hansatech oxygen electrode unit. Measurements of PPFD in CO_2 fixation experiments were made using a quantum sensor manufactured by Lambda Instruments (Model LI-185). For tobacco, the leaf absorptance when using either the red or white light source was calculated by measurement under the highest light level used in the experiment, the incident PPFD, the percentage light transmitted through the leaf, and assuming a leaf reflectance of 10%. For maize, the leaf absorptance was determined with an integrating sphere (10 cm diameter, Labsphere, North Sutton, NH) using an LED (for leaf

tissue used in O_2 exchange measurements) or a Schott's lamp (for leaf tissue used in CO_2 exchange and fluorescence measurements) as the light source as previously described (Oberhuber et al. 1993).

Results

Tobacco (Su/+ mutant)—The Su/+ mutant of tobacco had only ca. 30% as much Chl m^{-2} leaf as the wild-type; yet the leaf absorptance was only about 7% lower than the wild-type. The rate of photosynthesis per unit leaf area under saturating or near saturating levels of light was similar in the mutant and wild-type under normal ambient conditions. The mutant also had high rates of photosynthesis under non-photorespiring conditions, which on average were even higher than the wild-type under saturating light (Table 1). The maximum ϕ_{O_2} measured under non-photorespiring conditions with limiting levels of red light was also the same in the mutant and wild-type (Fig. 1).

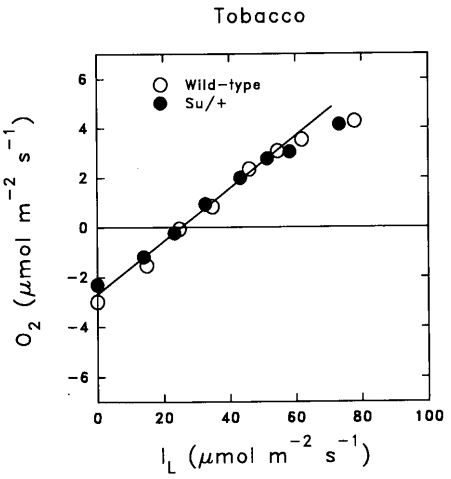

Fig. 1 Determination of maximum ϕ_{O_2} on an absorbed basis using red light with the Su/+ mutant (●) versus wild-type (○) tobacco leaves in an atmosphere of 1% CO_2. ϕ_{O_2} calculated from the initial slope is 0.106. The data are the average of two replications.

The light response curves for CO_2 fixation shown in Fig. 2 are typical in that the rates with the mutant are similar to the wild-type on a leaf area basis, although the mutant plants often required rather high light intensities to reach saturation. The mutant plants had much higher rates of photosynthesis than the wild-type on a Chl basis. In both mutant and wild-type, rates of photosynthesis over the range of light levels used were higher under a high CO_2, low O_2 atmosphere than under normal ambient conditions, due to suppression of photorespiration. It follows from these results, that in both the mutant and wild-type, ϕ_{CO_2} will decrease with increasing PPFD, and that at a given PPFD, ϕ_{CO_2} will be lower under photorespiring than under non-photorespiring conditions, as shown in Fig. 3. ϕ_{PSII} also decreased with increasing PPFD in a manner similar to ϕ_{CO_2}. However, at a given PPFD, with mutant and wild-type there was little or no difference in the value of ϕ_{PSII} between photorespiring and non-photorespiring conditions. The ratio of ϕ_{PSII}/ϕ_{CO_2} was reasonably constant over a range of light intensities; in both Su/+ and wild-type the ratio was higher under photorespiring than under non-photorespiring conditions (Fig. 3).

Maize (oil yellow Oy/+ mutant)—The oil yellow mutant (Oy/+) had about half the Chl content per unit leaf area as the wild-type, and a leaf absorptance about 9% lower than the wild-type (Table 2). The rate of photosynthesis in the mutant under saturating light was slightly less than that of the normal siblings on a leaf area basis, but the rate was much higher on a Chl basis. In both the mutant and wild-type, photosynthetic rates under saturating light were similar under normal ambient conditions and under low O_2, high CO_2 (Table 2), which indicates that neither the mutant nor the wild-type has any apparent photorespiration. Also, under limiting red light the maximum ϕ_{O_2} was similar in the wild-type and mutant (Fig. 4).

The light response curves for CO_2 fixation in the wild-

Table 1 Chl, leaf absorptance, and maximum rates of photosynthesis in tobacco Su/+ mutant and wild-type siblings

Type	Leaf Abs.	Leaf Chl (mg m^{-2})	Maximum photosynthesis rate			
			Normal air (μmol CO_2 m^{-2} s^{-1})	NPR atmosphere (μmol CO_2 m^{-2} s^{-1})	Normal air (μmol CO_2 g^{-1} Chl s^{-1})	NPR atmosphere (μmol CO_2 g^{-1} Chl s^{-1})
Wild-type	0.87	549	21.8	32.8	39.7	59.7
Mutant	0.80	188	22.2	38.5	118.1	204.8

Number of replications for leaf absorptance, Chl and photosynthesis rates were 2, 5, and 6 or more, respectively. Normal air was 340 μbar CO_2 and 21% O_2, NPR (non-photorespiratory) atmosphere was 675–800 μbar CO_2 and 2% O_2. The standard deviations for measurements of photosynthesis rates on a leaf area for wild-type (normal air), wild-type (NPR), Su/+ (normal air), and Su/+ (NPR) were 4.4, 5.0, 2.6 and 5.0, respectively. The maximum rates of photosynthesis were taken from light response curves where rates were saturating or near saturating (1,300–1,900 μmol quanta m^{-2} s^{-1}).

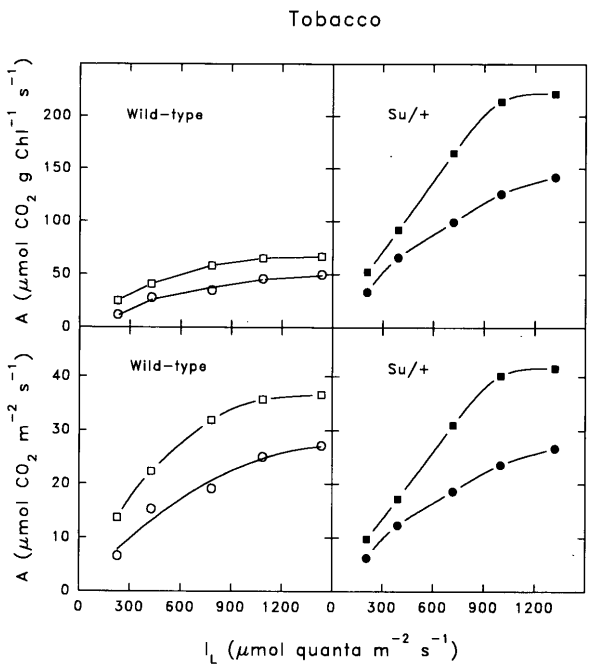

Fig. 2 Rates of photosynthesis of wild-type and mutant (Su/+) tobacco on a Chl and leaf area basis versus absorbed light intensity. The data is representative of light response curves obtained in different experiments. ●, ○, equals normal ambient atmosphere (340 μbar CO_2, 21% O_2); ■, □, equals non-photorespiratory atmosphere (675 μbar CO_2, 2% O_2).

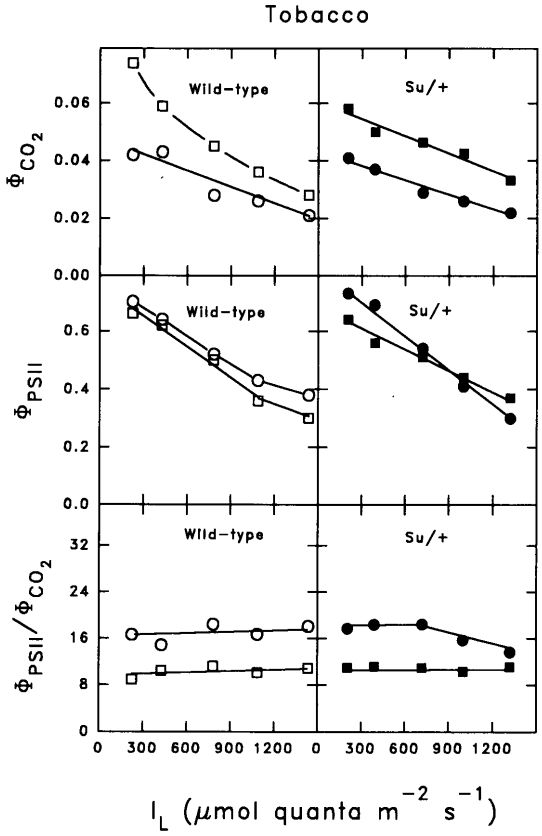

Fig. 3 The relationship between ϕ_{CO_2} and ϕ_{PSII} in wild-type and mutant tobacco (Su/+) under various intensities of absorbed light. ϕ_{CO_2} values $[(A+R_d)/I_L]$ were calculated from the data of Fig. 2 and with measured values of R_d of 2.98 and 2.29 μmol CO_2 m^{-2} s^{-1} for wild-type and mutant plants, respectively. ●, ○, equals normal ambient atmosphere (340 μbar CO_2, 21% O_2); ■, □, equals non-photorespiratory atmosphere (675 μbar CO_2, 2% O_2).

type and Oy/+ had a similar initial slope for photosynthesis on a leaf area basis, with slightly lower rates in the mutant under higher light intensities, whereas the mutant had clearly higher rates of photosynthesis on a Chl basis throughout the light response curve (Fig. 5). There was a nearly identical pattern of decline in ϕ_{PSII} values with increasing PPFD in the mutant and wild-type; there was a slightly greater decline in ϕ_{CO_2} values in the mutant with increasing light, due to its lower rate of photosynthesis on a leaf area basis. Consequently, the ϕ_{PSII}/ϕ_{CO_2} ratio was slightly higher in the mutant than in the wild-type, particularly at the highest light intensity (Fig. 6).

Table 2 Chl, leaf absorptance, and maximum rates of photosynthesis in maize Oy/+ mutant and wild-type siblings

Type	Leaf Abs.	Leaf Chl (mg m^{-2})	Maximum photosynthesis rate			
			Normal air (μmol CO_2 m^{-2} s^{-1})	NPR atmosphere (μmol CO_2 m^{-2} s^{-1})	Normal air (μmol CO_2 g^{-1} Chl s^{-1})	NPR atmosphere (μmol CO_2 g^{-1} Chl s^{-1})
Wild-type	0.85	407	26.3	29.9	68	70
Mutant	0.76	208	23.6	24.5	124	115

Number of replications for leaf absorptance, Chl and photosynthesis rates were 2, 8 and 8, respectively. Normal air was 340 μbar CO_2 and 21% O_2, NPR (non-photorespiratory) atmosphere was 1,000 μbar CO_2 and 2% O_2. The standard deviations for measurements of photosynthesis rates on a leaf area basis for wild-type (normal air), wild-type (NPR atmosphere), Oy/+ (normal air), and Oy/+ (NPR atmosphere) were 5.2, 5.0, 7.0 and 5.4 respectively. The maximum rates of photosynthesis were taken from light response curves at the highest level of incident light (1,200 μmol quanta m^{-2} s^{-1}).

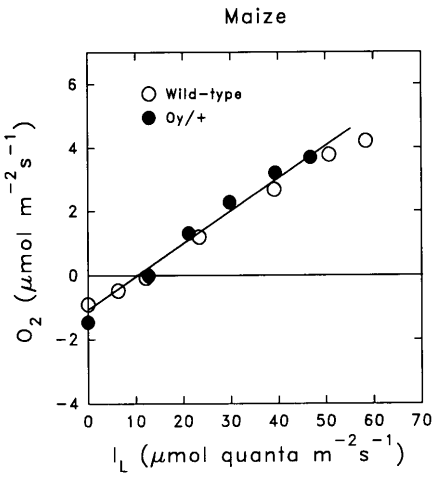

Fig. 4 Determination of maximum ϕ_{O_2} on an absorbed basis using red light with the Oy/+ mutant (●) versus wild-type (○) maize leaves in an atmosphere of 1% CO_2. ϕ_{O_2} based on the initial slope is 0.103.

Discussion

If a mutation in light harvesting Chl should cause a major imbalance of light absorption by the photosystems, then a significant reduction in the quantum yields of CO_2 fixation and PSII and a large change in the ϕ_{PSII}/ϕ_{CO_2} ratio would be expected (see eqn 1 in introduction). The present results indicate that it is possible to have a severe deficiency in Chl content in leaves of a C_3 and C_4 plant with little, or no, loss in the capacity for photosynthesis under saturating light, or in the quantum yields of CO_2 fixation and PSII over a range of light intensities.

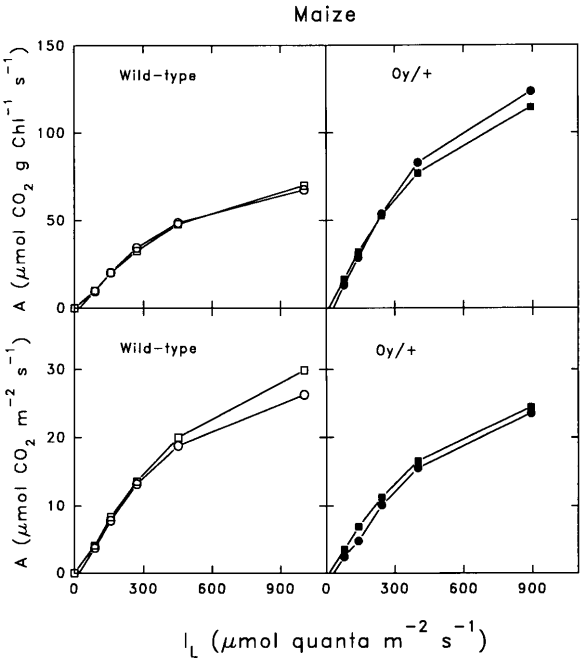

Fig. 5 Rates of photosynthesis of wild-type and mutant (Oy/+) maize plants on a Chl and leaf area basis versus intensity of absorbed light. The data is average of 4 separate experiments. ●, ○, equals normal ambient atmosphere (340 μbar CO_2, 21% O_2); ■, □, equals non-photorespiratory atmosphere (1,000 μbar CO_2, 2% O_2).

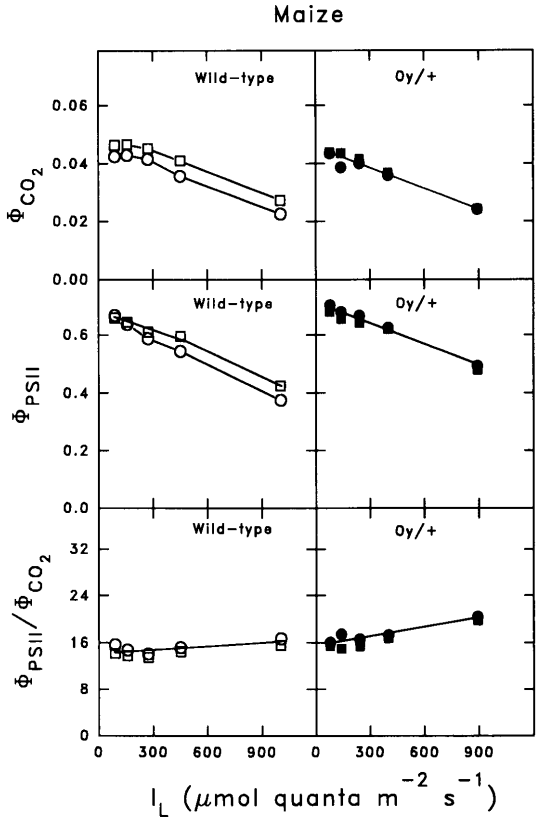

Fig. 6 The relationship between ϕ_{CO_2} and ϕ_{PSII} in wild-type and mutant maize (Oy/+) under various intensities of absorbed light. ϕ_{CO_2} values $[(A+R_d)/I_L]$ were calculated from the data of Fig. 5 and with measured values of R_d of 0.84 (+/− 0.57) and 1.18 (+/− 0.76) μmol CO_2 m^{-2} s^{-1} for wild-type and mutant plants, respectively. ●, ○, equals normal ambient atmosphere (340 μbar CO_2, 21% O_2); ■, □, equals non-photorespiratory atmosphere (1,000 μbar CO_2, 2% O_2).

C_3-tobacco (Su/+ mutant)—Su/+, a dominant aurea mutant of tobacco which is named for its visual similarity to plants lacking sulfur, was discovered by Burk and Menser (1964). The Chl content in leaves of the mutant was only 30% of the wild-type siblings (Table 1), similar to that seen in other studies, although the degree of deficiency is affected by growth conditions (Schmid 1967, 1971, Okabe et al. 1977). The CO_2 exchange rates and ϕ_{PSII} under varying light, and maximum quantum yield for O_2 evolution under limiting light, indicated that the severe reduction of Chl in the mutant has not impaired the efficiency of utiliza-

tion of absorbed energy for carbon assimilation. The maximum quantum yield for photosynthesis under limiting light and saturating CO_2, which can be determined most accurately with the leaf disc O_2 electrode system, was similar in the mutant and wild-type plants on the basis of absorbed red light (Fig. 1) or white light (not shown). This is not in agreement with Canaani et al. (1985) who, by photoacoustic analysis, reported that the mutant had higher relative quantum yields in red light, and lower relative quantum yields in blue light, than the wild-type plant. The lower quantum yield under blue light was suggested to be due to the mutant having a higher carotenoids/Chl ratio, and to the carotenoids being less efficient in light harvesting.

In general there is evidence that the Su/+ mutant has a high capacity for photosynthesis on a leaf area basis, equivalent to, or higher than, the wild-type under saturating light (see Schmid 1971). In the present study, rates were similar in mutant and wild-type under high light and under normal ambient atmosphere, while the mutant had higher rates under non-photorespiring conditions (Table 1). Schmid and Gaffron (1967) reported that the mutant can have a maximum rate of photosynthesis up to 2–3 times greater than the wild-type on a leaf area basis under high intensity red light (also see Canaani et al. 1985), but this difference was not observed by Okabe et al. (1977).

On a Chl basis, Su/+ tobacco has maximum photosynthesis rates several fold higher than the wild-type (Fig. 2, Schmid 1971, Okabe et al. 1977, Canaani et al. 1985). It appears that the mutation in Su/+ has only affected the photochemical apparatus, since the level of CO_2 fixing enzymes (Schmid and Gaffron 1967) and the kinetic properties of Rubisco (Koivuniemi et al. 1980) are the same in the mutant and wild-type.

Under non-photorespiring conditions (high CO_2 and low O_2), there is normally a high capacity for carbon assimilation via the dark reactions, so that photosynthesis is limited by the supply of energy and regeneration of RuBP. In the Su/+ mutant, it is possible that there is some compensation for the large loss of light harvesting Chl by an increase in some other components associated with PSII. This could allow higher rates of photochemistry, and consequently higher maximum rates of photosynthesis under non-photorespiring conditions in the mutant than the wild-type under saturating light intensities where light harvesting is not limiting (Table 1).

The aurea mutant, which is suggested to be better adapted to high PPFD, has unusual properties, including a high Chl *a/b* ratio (ca. two fold higher than the wild type in fully expanded leaves, Okabe et al. 1977), lower level of light harvesting pigments and the presence of agranal chloroplasts which may lack the structural separation of PSI and PSII found in the granal chloroplasts of normal siblings (Schmid and Gaffron 1967, Canaani et al. 1985).

The results of the present study indicate that the aurea mutant maintains a high efficiency in using absorbed energy, which indicates a balance in utilization by the two photosystems. Whether this is accomplished by structural changes in the position of the two photosystems in the thylakoids, changes in the light harvesting Chl of PSI as well as PSII, or in the relative numbers of reaction centers is uncertain. The thylakoids of the aurea mutant are deficient in an LHCP 28 kd protein (Specht et al. 1987, 1990). In the mutant, compared to the wild-type, the Hill reaction activity in isolated thylakoids and PSII complexes on a Chl basis is ca. 2 to 2.5 fold higher (Okabe et al. 1977, Specht et al. 1987, 1990); while the Chl content/reaction center (based on measurements of Mn and cyt_{b559}) in isolated PSII complexes is about 40% lower (Specht et al. 1987). The sizes of the photosynthetic unit of the wild-type and mutant as expressed by analysis of light flash experiments are 2,400 (+/− 700) and 600 (+/− 180) Chl CO_2 fixed^{-1} flash^{-1}, respectively (Okabe et al. 1977).

Another Chl deficit C_3 mutant which maintains a high capacity for photosynthesis is a temperature-sensitive, single recessive nuclear gene mutation of cowpea [*Vigna unguiculata* (L.) Walp] (Habash et al. 1990). Measurements of the efficiency of PSI and PSII show that it maintains a balance in efficiency of utilization of absorbed energy despite a 40% reduction in Chl content, an elevated Chl *a/b* ratio, and a decrease in polypeptides belonging to LHCII. The mutant and wild-type also had the same maximum ϕ_{O_2} on an absorbed light basis, the same number of PSII units per leaf area, and the leaf absorptance in the mutant was only 11% lower than the wild-type (Habash et al. 1990). Thus, like the aurea mutant of tobacco, the cowpea mutant maintains a high efficiency in utilization of absorbed energy for photosynthesis.

The chlorina mutant of the C_3 plant barley is a Chl *b*-less mutant which lacks the light harvesting Chl *a/b* complex. Unlike the aurea tobacco mutant, and the temperature sensitive cowpea mutant, the chlorina mutant of barley has a substantially lower ϕ_{O_2} under limiting light and a higher ϕ_{PSII}/ϕ_{CO_2} ratio than the wild-type (Öquist and Chow 1992). In this case, the deficiency in light harvesting capacity of PSII in the mutant may result in energy distribution of the two photosystems being out of balance.

C_4-maize (Oy/+)—The oil yellow mutant of maize (Oy/+) has a block in its conversion of protoporphyrin IX to Mg-protoporphyrin which limits Chl synthesis, but the exact location of the mutation is not known (Mascia 1978). There are two viable alleleic variations of this mutant, including a heterozygous dominant (Oy/+) and a homozygous recessive (oy/oy). These yellow-green mutants are deficient in Chl *b* (the Chl *a/b* ratio is ca. 1.5 fold higher in Oy/+ than the wild type, Jenkins et al. 1989), the light harvesting Chl *a/b* proteins and they have lower levels of the 23 and 25 kd thylakoid polypeptides (Miles et al. 1979,

Hopkins et al. 1980a). In separate assays, the activities of both PSI and PSII in isolated chloroplasts were ca. 3 times higher in the mutant than the wild-type on a Chl basis (Hopkins et al. 1980b). Maximum rates of photosynthesis under high light in the mutant on a leaf area basis are similar, or slightly lower, than that of the wild-type, while rates on a chlorophyll basis are much higher in the mutant than the wild-type (Fig. 5, Jenkins et al. 1989). It was previously shown that the mutant when grown under high light had a lower level of photosynthetic enzymes which accounted for slightly lower light-saturated rates of photosynthesis on a leaf area basis (Jenkins et al. 1989).

The present study shows that the Oy/+ mutant and wild-type had similar maximum quantum yield for photosynthesis under limiting light. Also, in both, ϕ_{PSII} and ϕ_{CO_2} decreased in a similar manner with increasing PPFD. The mutant had a slightly higher ϕ_{PSII}/ϕ_{CO_2} ratio than the wild-type at a given I_L. Why the ratio is higher in the mutant under high light is uncertain; it could reflect either an increase in electron sinks (hence an increase in J_e/A^*) or a slightly lower fraction of light being absorbed by PSII (see eqn 1 in Introduction). However, the degree of similarity in the ϕ_{PSII}/ϕ_{CO_2} ratios overall can be explained by the leaf absorptance in the mutant being only 9% lower than in the wild-type, and by the mutant largely maintaining a balanced absorption of light between PSI and PSII. Yet how a balance in absorption and utilization of energy between the photosystems can be maintained in the mutant is uncertain. As a consequence of the Chl deficiency there may be changes in light harvesting in both photosystems. Greene et al. (1987) suggested there is a selective loss of the mobile Chl *a/b* LHCII complexes and a decrease in the PSI light harvesting antennae in the Oy/+ mutant. Modifications in the light harvesting associated with both photosystems could explain how a balance is maintained in absorption and utilization of light. The mobile light harvesting LHCII complex is suggested to serve as both light harvesting antenna and a membrane adhesion factor, which would explain why the mesophyll chloroplasts of the mutant tend to be agranal (Hopkins et al. 1980a). Since bundle sheath chloroplasts of wildtype maize have little development of grana and low photosystem II (Edwards and Walker 1983), the oil yellow mutation may have a primary effect on mesophyll chloroplasts.

High photosynthetic efficiencies in Chl deficient mutants—In conclusion, there are Chl deficient mutants which, despite having a 40 to 70% lower Chl content, a high Chl *a/b* ratio, a lower level of certain Chl binding proteins of PSII and a decrease in LHCII complexes, maintain a high efficiency of CO_2 fixation and a high quantum yield of PSII similar to wild-type plants. This may be explained partly by the fact that a reduction in Chl content of the leaf results in a less than proportional decrease in leaf absorptance due to a curvilinear relationship between absorptance and Chl content (Gabrielson 1948). A 50–70% reduction in Chl content in the aurea tobacco and oil yellow maize mutants results in only a 7–9% reduction in leaf absorptance. If this decrease in Chl content resulted in a strong preferential decrease in absorptance of light by PSII, then a measurable decrease in efficiency in utilizing quanta in photosynthesis would be expected due to the imbalance of absorption of energy between the photosystems unless there are other compensating changes. Means by which these mutants maintain high quantum yields for photosynthesis, equivalent to the wild-type plants, remain to be determined.

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