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THE RELATIVE ABSORPTION CROSS-SECTIONS OF PHOTOSYSTEM I AND PHOTOSYSTEM II IN CHLOROPLASTS FROM THREE TYPES OF *NICOTIANA TABACUM*

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Summary

In the present study we used three types of *Nicotiana tabacum*, cv John William's Broad Leaf (the wild type and two mutants, the yellow-green Su/su and the yellow Su/su var. Aurea) in order to correlate functional properties of Photosystem II and Photosystem I with the structural organization of their chloroplasts. The effective absorption cross-section of Photosystem II and Photosystem I centers was measured by means of the rate constant of their photoconversion under light-limiting conditions. In agreement with earlier results (Okabe, K., Schmid, G.H. and Straub, J. (1977) Plant Physiol. 60, 150—156) the photosynthetic unit size for both System II and System I in the two mutants was considerably smaller as compared to the wild type. We observed biphasic kinetics in the photoconversion of System II in all three types of *N. tabacum*. However, the photoconversion of System I occurred with monophasic and exponential kinetics. Under our experimental conditions, the effective cross-section of Photosystem I was comparable to that of the fast System II component (α centers). The relative amplitude of the slow System II component (β centers) varied between 30% in the wild type to 70% in the Su/su var. Aurea mutant. The increased fraction of β centers is correlated with the decreased fraction of appressed photosynthetic membranes in the chloroplasts of the two mutants. As a working hypothesis, it is suggested that β centers are located on photosynthetic membranes directly exposed to the stroma medium.

Abbreviations: Chl, chlorophyll; *P*-700, the primary donor of Photosystem I; Q, the primary acceptor of Photosystem II; DCMU, 3-(3,4-dichlorophenyl)-1,1-dimethylurea; Tricine, *N*-tris(hydroxymethyl)methylglycine.

Introduction

One intriguing aspect of the structural and functional organization in the higher plant chloroplast is the microscopic complexity of its photosynthetic membranes [1,2]. Thus, chloroplasts from different species of higher plants possess a varying amount of appressed photosynthetic membranes (at the partitions of the grana) with respect to those membranes that are exposed to the stroma medium (stroma lamellae and grana margins) [3—5]. In addition, the effective absorption cross-sections of Photosystem II and Photosystem I (size of the photosynthetic units) has also been shown to vary depending on the plant growth conditions, plant age and/or chloroplast development state [5—10]. Such variations in the chloroplast ultrastructure and photosynthetic unit size can also be caused by mutations [11—14].

The effect of mutations on photosynthetic parameters of tobacco chloroplasts (*Nicotiana tabacum*, cv John Williams's Broad Leaf) have been studied by Schmid and his coworkers [7,15—18]. The main two mutants that have been isolated (the yellow-green Su/su and the yellow Su/su var. Aurea [18]), show an ultrastructure with more extended intergrana (or stroma thylakoid) regions and considerably less partition regions than the wild type [15,17,18]. In addition, they show higher Chl *a*/Chl *b* ratios and a considerably decreased photosynthetic unit size. The above parameters have been affected more severely in the yellow Su/su var. Aurea type than in the yellow-green Su/su.

Recent publications have suggested a heterogeneity in the reaction centers of Photosystem II in isolated chloroplasts [19—25]. The two reaction center complexes (referred to as α centers and β centers) that were kinetically distinguished differed, among other things, in their effective absorption cross-section [21—23] and the midpoint redox potential of their primary electron acceptor [24,25]. In the present study, working with chloroplasts isolated from the above-mentioned three types of *N. tabacum*, we compared the photoconversion kinetics of System II with those of System I. Under continuous excitation conditions, we detected monophasic exponential kinetics for the conversion of System I. However, the conversion kinetics of System II were biphasic. A method for the comparative study of the effective absorption cross-sections of System I and System II is presented. The functional properties of the three types of chloroplasts are correlated with the structural organization of their photosynthetic membranes.

Materials and Methods

Chloroplasts were isolated from leaves of three types of *N. tabacum*, cv John William's Broad Leaf (the wild type and two mutants, the yellow-green Su/su and the yellow Su/su var. Aurea). The plants were cultivated in the laboratory under controlled conditions. The chloroplast isolation procedure has been described earlier [22]. The sample chlorophyll concentration and the Chl *a*/Chl *b* ratios were determined according to Arnon [26]. The reaction mixture contained chloroplasts suspended in the isolation buffer (0.4 M sucrose, 50 mM Tricine, 10 mM KCl and 5 mM $MgCl_2$, pH 7.8) at a chlorophyll concentration of approximately 100 μg/ml for the kinetic experiments. The optical path-

length of the sample was approximately 1.2 mm.

Measurements of the chloroplast fluorescence induction kinetics at 685 nm, the kinetics of *P*-700 photobleaching and the reduction kinetics of the primary electron acceptor Q of Photosystem II were performed with the same apparatus operated as a fluorometer and as a split-beam absorbance difference spectrophotometer. For the *P*-700 measurements the temperature of the sample was lowered to −57°C. The method employed in these measurements has been described previously [27,28]. For the above experiments, actinic illumination was provided in the green region of the spectrum by a combination of CS 4-96 and CS 3-67 Corning filters. In all kinetic experiments, the actinic light intensity was approximately 1.8 mW · cm^{-2}. Signal averaging was accomplished with a Nicolet Instrument Co., Model 527.

Results

Chloroplasts isolated from the tobacco Su/su mutant or the Su/su var. Aurea mutant have a decreased amount of chlorophyll and considerably less extensive system of photosynthetic membranes [15—18]. An indirect insight in the chlorophyll content and photosynthetic membrane density of the chloroplasts isolated from the three types of tobacco was obtained by measuring the absorption spectra of the chloroplasts. Fig. 1 compares the absorption spectra of tobacco wild-type chloroplasts with those of the Su/su var. Aurea mutant. The two spectra were arbitrarily normalized at 680 nm. An obvious difference

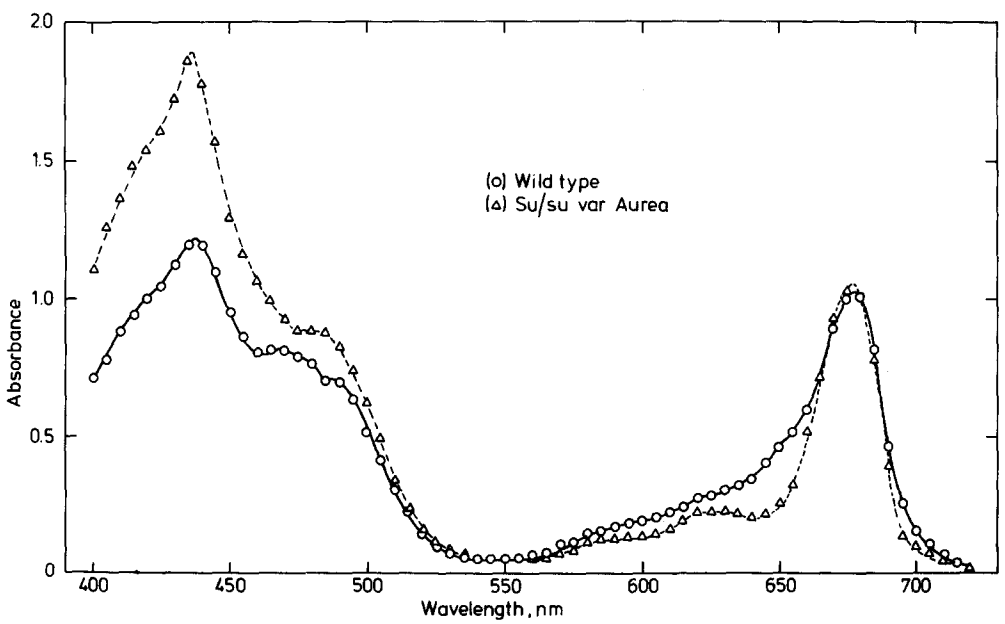

Fig. 1. Absorbance spectra of the tobacco wild-type (○) and of the Su/su var. Aurea (△) chloroplasts arbitrarily normalized at 680 nm. The two spectra were measured in a Cary 14 spectrophotometer by the 'opal glass' method and have been corrected for scattering from the absorption readings in the wavelength region between 740 and 800 nm. Note the absorbance contribution from chlorophyll *b* around 650 nm and the suppressed Soret band of the wild-type chloroplasts.

between the two spectra is the contribution of the Chl *b* absorption in the wavelength region between 600 and 660 nm in the wild type. Table I gives some typical values of the Chl *a*/Chl *b* ratio for the three types of chloroplasts. The above quoted values were found to vary from preparation to preparation depending on the age of the plant and on the leaf size [18] but in general they remained within a fixed range (wild type, 2.2—3.0; Su/su 35—5.5; Su/su var. Aurea 5.0—10.0). A similar variation was observed in the value of the other parameters measured in this work (see below). Another pronounced difference between the two spectra (Fig. 1) is the surpressed Soret band of the wild type which is explained by the lower content in carotenoids [18] and by the strong particle flattening of these chloroplasts. We have calculated the flattening correction factors at 435 nm for the three types of chloroplasts according to the method given by Pulles et al. [29] to be 2.2 for the wild type, 1.5 for the yellow-green Su/su mutant and 1.13 for the yellow Su/su var. Aurea mutant (see Table I). The differential flattening correction factors at 320 nm were estimated by the same method and found to be 1.9 for the wild type, 1.3 for the yellow-green Su/su mutant and 1.1 for the yellow Su/su var. Aurea mutant (see also Table I). These values also varied slightly from preparation to preparation.

The effective absorption cross-section of a reaction center complex would depend on the efficiency of excitation energy transfer to the reaction center, on the efficiency of charge separation at the reaction center and also on the number of chlorophyll molecules that transfer excitation energy to the particular reaction center. For the purpose of this publication we assumed that the product of the first two parameters is approximately the same for all reaction centers, most likely a value close to unity (see below). Then, a relative measure of the effective absorption cross-section of the antenna associated with Photosystem II and Photosystem I centers is given from the rate constant of their photoconversion under weak continuous illumination. In order to measure the photoconversion rate of System I centers, we preilluminated dark-adapted chloroplasts for a few seconds with continuous light in the presence of 15 μM 3-(3,4-dichlorophenyl)-1,1-dimethylurea (DCMU) and 2 mM hydroxylamine at 0° C. Subsequently, the temperature of the sample was lowered to −57° C. Under these conditions, the photooxidation of *P*-700 is reversible but electron transport components located between the two photosystems either remain oxidized or, if reduced, they cannot transfer an electron to *P*-700 [27,28,30]. Therefore, illumination at −57° C induces the transfer of only one electron from *P*-700 to the acceptor side of System I. Fig. 2A shows the photobleaching of *P*-700 under the above-mentioned conditions. From the amplitude of the absorbance change at 700 nm and from the extinction coefficient of *P*-700 given by Ke [31] we have calculated that approximately 430 chlorophyll molecules (*a* and *b*) are present per *P*-700 molecule in the wild type. A similar value was determined from measurements at room temperature in the presence of ascorbate and methyl viologen. Table I shows the total number of chlorophyll molecules per reaction center of System I (Chl/*P*-700) in the three types of chloroplasts. The kinetics of *P*-700 photobleaching were monophasic exponential functions of time in all types of tobacco chloroplasts but the rate of their photoconversion was considerably slower in the two mutants than in

TABLE I

PHOTOSYNTHETIC PARAMETERS OF TOBACCO CHLOROPLASTS

Chlorophyll concentration and flattening correction factors at 435 and 320 nm were determined according to Refs. 26 and 29, respectively. The *P*-700 concentration was determined spectrophotometrically at 700 nm [31] with chloroplasts in the presence of 15 μM DCMU, 1 mM ascorbate, 10 μM 2,6-dichlorophenolindophenol and 50 μM methyl viologen. The Q concentration was measured also spectrophotometrically at 320 nm [35] with chloroplasts in the presence of 15 μM DCMU and 1.0 mM $K_3Fe(CN)_6$. The value of β_{max} and the rate constants k_α, k_β and $k_{P\text{-}700}$ were determined from the semilogarithmic plots of Fig. 5. The rate constants are proportional to the absorption cross-section of the respective centers.

	Chl *a*/Chl *b*	Flattening correction factor at 435 nm	Differential flattening correction factor at 320 nm	Chl/*P*-700	Chl/Q	β_{max} (% of total)	k_β (s^{-1})	k_α (s^{-1})	$k_{P\text{-}700}$ (s^{-1})
wild type	2.8	2.2	1.9	430	220	40	8.3	17.3	15.7
Su/su	4.7	1.5	1.3	330	120	58	2.1	11.0	11.3
Su/su var. Aurea	5.7	1.13	1.1	300	75	71	2.3	9.1	9.3

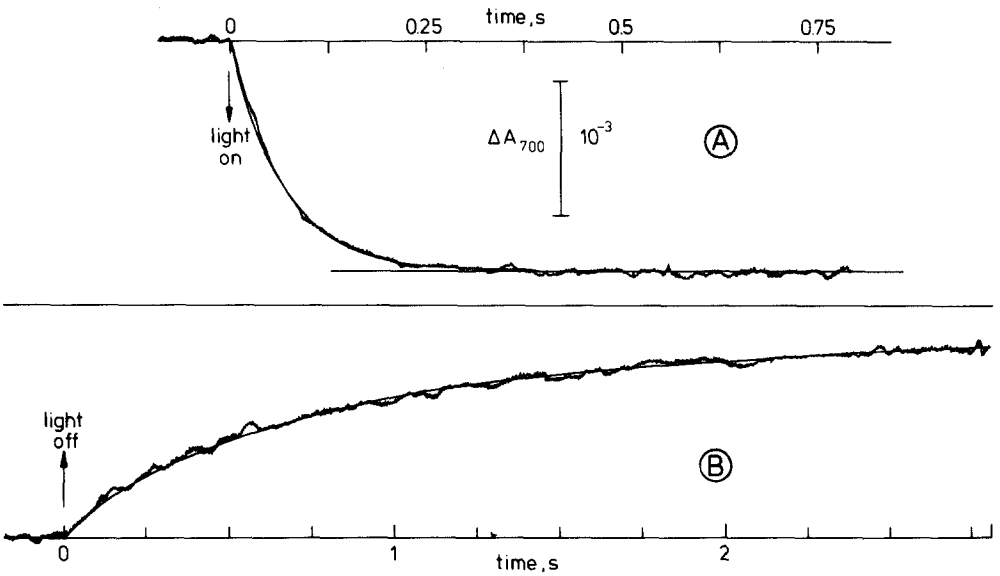

Fig. 2. (A) The kinetics of *P*-700 bleaching of wild-type tobacco chloroplasts at −57°C. The chloroplasts were suspended in a glycerol medium [27] in the presence of DCMU and hydroxylamine. They were preilluminated at 0°C for 2 s with continuous light. (B) The kinetics of *P*-700 restoration at −57°C. The full restoration of *P*-700 occurred within 10—15 s.

the wild type (see below). Fig. 2B shows the kinetics of *P*-700 restoration upon turning off the actinic illumination [28]. It was found that the restoration occurred with kinetics considerably slower than the light-induced bleaching. The restoration process was kinetically identical for the three types of tobacco chloroplasts and also independent of the actinic illumination (a 10 μs flash up to 2 s continuous illumination).

It has been found that in the temperature region between −50 and −60°C the photochemical properties and the functional organization of the photosynthetic units are similar to those at room temperature [32,33]. Therefore, the results obtained at −57°C can be directly compared to those obtained at room temperature. Experiments at room temperature, in the presence of DCMU and sufficient ferricyanide to oxidize the electron carriers between the two photosystems, showed that the rate constant for *P*-700 photobleaching was the same as at −57°C. However, in the presence of ferricyanide, the amplitude of the signal indicated the light-induced turnover of a smaller fraction of *P*-700 (approximately 10—50% of the total depending on the ferricyanide concentration), presumably due to the chemical (dark) oxidation of *P*-700 by the oxidant [22,23]. We avoided working at room temperature in the absence of any oxidant because, under such conditions, we could not completely eliminate any secondary electron transfer to P^+-700 from other electron carriers (for example from cytochrome *f*).

The photoconversion rate of System II centers was measured at room temperature with dark-adapted chloroplasts in the presence of DCMU and hydroxylamine by means of the fluorescence induction curve. Fig. 3 shows the fluorescence induction kinetics obtained with the three types of tobacco

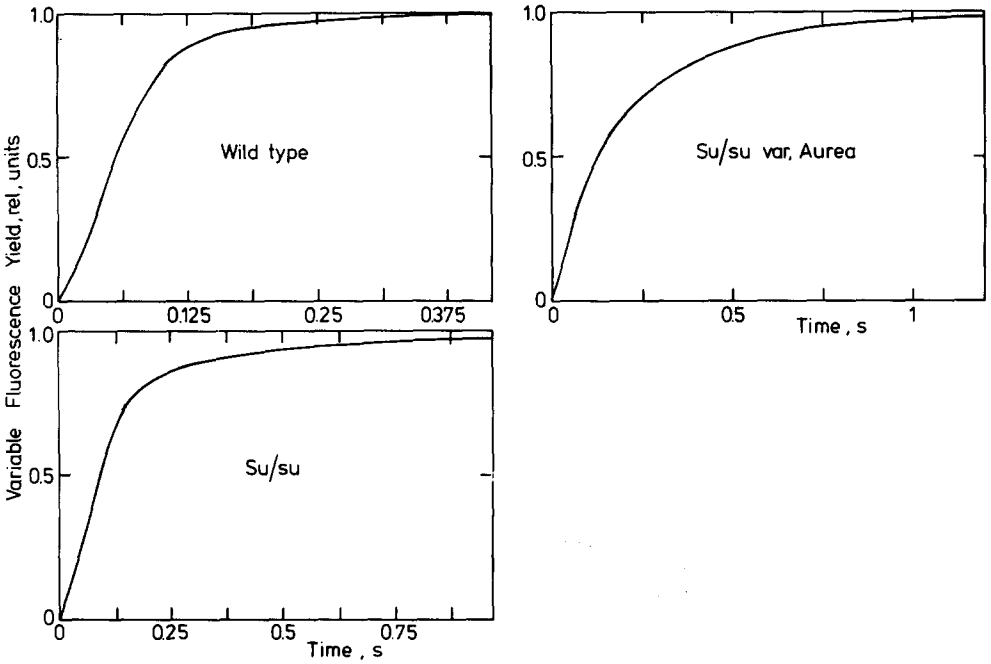

Fig. 3. The kinetics of the variable fluorescence yield of chloroplasts from three varieties of tobacco plants normalized to the same F_0 ($F_0 = 0$) and F_{max} ($F_{max} = 1$) relative values. The chloroplasts were illuminated in the presence of 15 μM DCMU and 2 mM hydroxylamine by green actinic light of the same intensity. Note the difference in the three time scales.

chloroplasts. They all show the well-known initial sigmoidal rise which is followed by the slow β phase [19], or tail [34]. However, the fluorescence rise curve of the yellow-green Su/su mutant shows a proportionally larger contribution of the slow β phase (lasting from 0.2 s to the end of the induction phenomenon) with respect to that of the wild type. In the yellow Su/su var. Aurea mutant the sigmoidal part is barely discerned because the fluorescence induction curve is dominated by the exponential β phase. In addition to the above-reported changes, it is observed that the induction phenomenon becomes progressively slower in the two mutants.

In order to obtain a more quantitative estimate of the mutation-induced changes on the two System II kinetic components, as well as to compare directly the rates of System II and System I photoconversion, we measured the area growth over the fluorescence induction curve [19,21—23]. Fig. 4 compares directly the kinetics of Q^- accumulation, as measured by the area growth, with the kinetics of *P*-700 bleaching for the Su/su mutant. The two parameters have been normalized to the same amplitude. It is observed that the *P*-700 photobleaching reached the steady-state level sooner than the photoreduction of Q. Fig. 5 compares, in a semilogarithmic plot, the kinetics of Photosystem I and Photosystem II for the three types of chloroplasts. As mentioned earlier, the kinetics of System II energy conversion were biphasic. The intercept of the linearly extrapolated slow phase with the ordinate at zero time gave a relative measure of the total contribution of the slow phase to the kinetics (β_{max} in

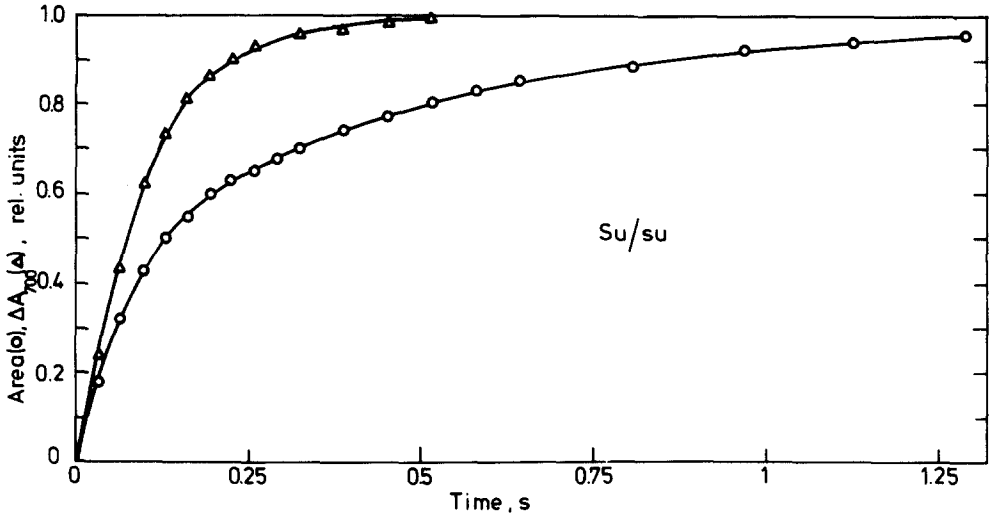

Fig. 4. Kinetics of the area growth over the variable fluorescence curve (○) and of the *P*-700 photobleaching (△) of chloroplasts isolated from the Su/su type of tobacco. The two parameters have been normalized to the same relative amplitude.

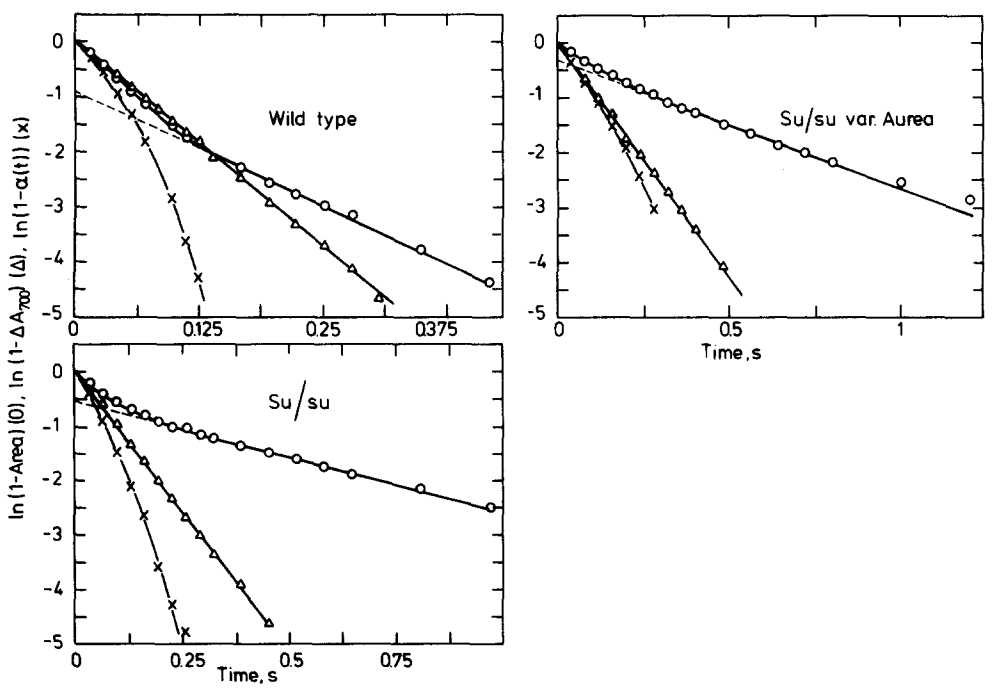

Fig. 5. A semilogarithmic plot of the kinetics of the biphasic area growth over the fluorescence induction curve (○), of the *P*-700 photobleaching (△) and of the fast α component of the area growth (X) of chloroplasts from the three types of tobacco. Note the difference in the three time scales.

Table I). The value of β_{max} for the wild type was equal to 40%. It was increased to 58% and 71%, respectively, in the Su/su and Su/su var. Aurea chloroplasts. These results could not be attributed to incomplete blocking by DCMU or to a fast charge recombination (back reaction) since a 10 μs saturating flash invariably eliminated more than 90% of the area over the fluorescence induction curve. By measuring the kinetics of absorbance change at 320 nm [22], we verified that the two phases of area growth shown in all of the above measurements did correspond to two phases of the same relative amplitude in the reduction of plastoquinone molecules to anionic plastosemiquinone [35]. From the amplitude of the absorbance change at 320 nm (corrected for particle flattening at this wavelength) and from the extinction coefficient of the primary electron acceptor Q of Photosystem II given by Van Gorkom [35] we have calculated that approximately 220 chlorophyll molecules are present per Q in the wild type. The corresponding values for the Su/su and Su/su var. Aurea mutants were 120 and 75, respectively. These values, if compared with the corresponding ones of System I (see Table I Chl/*P*-700 and Chl/Q) show that in the mutants, especially in the Su/su var. Aurea, the ratio of System I to System II (*P*-700/Q) is considerably lower than in the wild type. It may be concluded that a direct effect of the mutation was on the stoichiometry of system I and system II reaction centers.

Table I shows the values of the rate constant k_β as measured from the slopes of the slow phase in the logarithmic plot of Fig. 5. The value of k_β is proportional to the absorption cross-section of the β centers. It is decreased approximately 4-fold in the Su/su, with respect to the wild type, but is not further changed in the Su/su var. Aurea chloroplasts. Fig. 5 (crosses) shows the kinetics of the fast System II component (α component) obtained from the overall System II kinetics by subtracting the contribution of the slow phase [20,22]. The deviation of the α component from linearity corresponds to the sigmoidicity of the fluorescence induction curve (see Fig. 3) and is compatible with a statistical pigment-bed model for System II centers [21—23]. An estimate of the absorption cross-section (per center) for the centers in the statistical pigment bed was obtained from the initial slope of the α component (k_α in Table I).

As mentioned earlier, the photoconversion of *P*-700 was an exponential function of time. Fig. 5 (triangles) shows logarithmic plots of the *P*-700 kinetic data. Table I shows the first-order rate constants $k_{P\text{-}700}$ for *P*-700 photoconversion calculated from the logarithmic plots of Fig. 5.

The results of Table I, and those of Fig. 5, show that the absorption cross-sections of Photosystem I closely correspond to those of the α centers of Photosystem II and that both absorption cross-sections were decreased by about 30% in the yellow-green Su/su and by 40—50% in the yellow Su/su var. Aurea chloroplasts with respect to that of the wild type. The possible meaning of these results will be discussed below.

Discussion

The results presented in this work show that, under continuous excitation conditions, the photoconversion kinetics of System I are monophasic exponen-

tial functions of time while the kinetics of System II are biphasic. This basic property was observed with chloroplasts isolated from the two mutant plants as well as from the wild-type tobacco. The assignment of the two kinetic components of System II to photoconversion of centers in separate units (β centers) and in a statistical pigment bed (α centers) has been discussed earlier [21—23]. The exponential photoconversion kinetics of System I are also compatible with a model of separate units for this photosystem. However, a more likely explanation is that System I units form a statistical pigment bed in which the oxidized *P*-700 is an efficient excitation quencher thus preventing energy transfer between neighbouring System I units [14,36].

A pronounced difference between the three types of chloroplasts involved the absorption cross-sections of the two mutants as compared to that of the wild type. According to the results of Table I ($k_{P\text{-}700}$ and k_α) the number of chlorophyll molecules present per *P*-700, or per α center, was decreased by about 30% in the Su/su and by about 40—50% in the Su/su var. Aurea chloroplasts. The number of chlorophyll molecules present per β center was similar in the two mutants although decreased by about 75% of that of the wild type (k_β in Table I). It is also interesting to observe, by comparing the values of k_α and k_β in Table I, that in the wild type the apparent absorption cross-section of the α centers is about twice that of the β centers. In the mutants, however, the α centers have an absorption cross-section 5—6 times larger than that of the β centers.

The present work also shows that the ratio of α centers to β centers was decreased in the two mutants (see β_{max} in Table I). In different chloroplast preparations from the wild type the β centers accounted from 25 to 45% of the total number of Photosystem II centers. In the chloroplasts isolated from the mutant plants there were considerably more β centers than α centers (see β_{max} in Table I). As pointed out in Results, a change in the β_{max} value reflected a change in the relative concentration of the β centers and not merely a change in the yield of fluorescence associated with the two centers. The relative concentration of the β centers in the three types of chloroplasts could be directly correlated with the chloroplast ultrastructure and/or with the Chl *a*/Chl *b* ratio. Electron micrographs from the wild-type tobacco have shown chloroplasts with a well-developed system of grana and relatively few intergrana membranes [7,15,17]. To the contrary, the Su/su chloroplasts exhibited a considerably less dense system of grana and rather expanded intergrana, or stroma thylakoid, regions. The obvious consequence of the mutation was a relatively larger membrane area directly exposed to the stroma medium. In the Su/su var. Aurea chloroplasts the intergrana regions were more extended and, on the average, the number of individual thylakoids participating in the formation of a granum was further decreased [15,17]. Since Chl *b* molecules are predominantly located on the partitions of the grana [37] the increase in the Chl *a*/Chl *b* ratio observed in the chloroplasts of the Su/su var. Aurea (see Table I, also Ref. 18) could be directly attributed to the decreased grana content in these chloroplasts, or vice versa. These observations indicate that the β centers become predominant in the chloroplast when the intergrana membranes become more numerous and/or when the amount of Chl *b*-containing light-harvesting complex in the chloroplast is decreased. It is suggested that β centers may be located on photo-

synthetic membranes directly exposed to the stroma medium while α centers may be located in the partitions of the grana. Such an idea, which can serve as a working hypothesis, was presented earlier [21] on the basis of the effect of thylakoid unstacking on the kinetic properties of the α and β centers. In an earlier work with developing chloroplasts [8] it was concluded that the appearance of heterogeneity in Photosystem II preceded the formation of grana. The possibility remained, however, that in those developing photosynthetic membranes there was an early differentiation in areas that would eventually become partitions of a granum and areas that would remain as free or stroma-exposed lamellae in the matured chloroplast.

An interesting observation in the three types of chloroplasts was the similar cross-section of the α centers and of *P*-700 (see k_α and $k_{P\text{-}700}$ in Table I). It is implied that, under our experimental conditions, α centers and *P*-700 receive approximately equal amounts of excitation energy from their surrounding antenna molecules which presumably include Chl *a* and Chl *b* [21,22,25]. One might speculate that the α centers and *P*-700 are located in the same statistical pigment bed where they compete for the available excitation energy with equal efficiency. Alternatively, the regulatory function for the equal distribution of excitation between α centers and *P*-700 could be performed by the Chl *b*-containing light-harvesting complex as proposed by Butler and Strasser [38]. However, assuming that our System I measurements reflected the photoconversion of *P*-700 in both the stroma and grana thylakoids, the above considerations do not easily explain the monophasic kinetics of *P*-700 which imply that the effective cross-section of *P*-700 is the same in the stroma and grana lamellae. The same is true for the stoichiometry of System I to System II centers. Using the results presented in Table I one can calculate that the stoichiometric ratio *P*-700/Q_α of System I centers to α centers was approximately the same in the three types of chloroplasts. To the contrary, the stoichiometric ratio *P*-700/Q_β of System I centers to β centers was lower by a factor of 2 in the Su/su and lower by a factor of 4 in the Su/su var. Aurea when compared to that of the wild type. At this stage it is difficult to completely evaluate the causal relationship between the stoichiometric ratio of Photosystem I/Photosystem II, the absorption cross-section changes and the change in the Chl *a*/Chl *b* ratio with the mutation-induced structural changes. Clearly more work in this direction is required. One can also point out that although the higher plant chloroplast differentiation in areas of stroma and grana thylakoids is well established, nothing is known about the functional meaning of this differentiation. One can speculate that membranes exposed to the stroma medium may play a different physiological role than the membranes at the partitions of the grana. In this context, the physiological significance of the β centers is possibly of great importance and needs to be further investigated.

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