Photosynthesis and Respiration in Cyanobacteria

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Secondary article

Article Contents

Cyanobacteria are among the very few groups that can perform oxygenic photosynthesis and respiration simultaneously in the same compartment, and some cyanobacterial species are able to fix nitrogen. This combination of metabolic pathways is unusual and this metabolic flexibility may be responsible for the evolutionary hardiness of the cyanobacteria and their ability to thrive under a wide range of conditions.

Introduction

Cyanobacteria (formerly known as blue-green algae) are thought to be among the evolutionarily oldest organisms: putative microfossils have been found that are 3.5 billion years old and that are attributed to cyanobacteria (Schopf, 1993). A main reason for the evolutionary hardiness of cyanobacteria is their successful combination of effective metabolic pathways. They are among the very few groups that can perform oxygenic photosynthesis and respiration simultaneously in the same compartment, and many cyanobacterial species are able to fix nitrogen. Therefore, they can survive and prosper under a wide range of environmental conditions.

The combination of photosynthesis and respiration in a single compartment is thought to be quite unique, and the ramifications of this combination are reviewed. Photosynthesis and respiration require electron transport pathways that to a large extent are catalysed by protein complexes in membranes. **Figure 1** illustrates the compartmentalization of the cyanobacterial cell. The thylakoid membrane, the internal membrane system that separates the cytoplasm from the lumen and that is present in virtually all cyanobacteria, contains both photosynthetic and respiratory electron transport chains. These electron transport chains intersect, and in part utilize the same components in the membrane. Note that oxygenic photosynthesis (conversion of CO_2 and water to sugars using the energy from light) essentially is the reverse of respiration (conversion of sugars to CO_2 and water releasing energy). The cytoplasmic membrane, separating the cytoplasm from the periplasm, contains a respiratory electron transport chain but not photosynthetic complexes in most cyanobacteria. Therefore, in most cyanobacteria, photosynthetic electron transport occurs solely in thylakoids, whereas respiratory electron flow takes place in both the thylakoid and cytoplasmic membrane systems. Overviews regarding aspects of cyanobacterial biochemistry and molecular biology related to photosynthesis and respiration are provided in Gantt (1994) and Schmetterer (1994).

The presence and simultaneous activity of photosynthetic and respiratory electron transport chains in the same membrane system is unusual. A schematic representation of the respiratory and photosynthetic electron transport chains in cyanobacterial thylakoid membranes is shown in **Figure 2**. As indicated, cyanobacteria utilize several redox-active components in thylakoids for both photosynthesis and respiration, including the plastoquinone (PQ) pool, the cytochrome b_6f complex, and the soluble electron carriers in the lumen (in most species primarily plastocyanin, but cytochrome c_{553} (also known as cytochrome c_6) also occurs). In any case, the common use of components

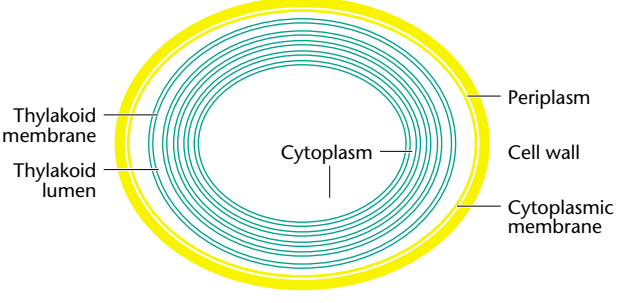

Figure 1 Outline of membranes and compartments in a cyanobacterial cell. The cytoplasmic membrane separates the cytoplasm from the periplasm; this membrane system is involved in respiration but not in photosynthesis, and is yellow due to the presence of carotenoids. Thylakoid membranes catalyse both photosynthetic and respiratory electron transport; they contain chlorophyll and therefore are green. Thylakoids are vase-shaped, and occur in pairs (the view represented here corresponds to a cross-sectional cut through the vase). One pair of membranes envelops the next pair, much like a set of Russian dolls. The space between a pair of thylakoid membranes is the thylakoid lumen, into which protons are deposited upon photosynthetic and respiratory electron transport in thylakoids. The resulting proton gradient across the thylakoids is used for ATP synthesis. The space between two pairs of thylakoids is contiguous with the cytoplasm of the cell.

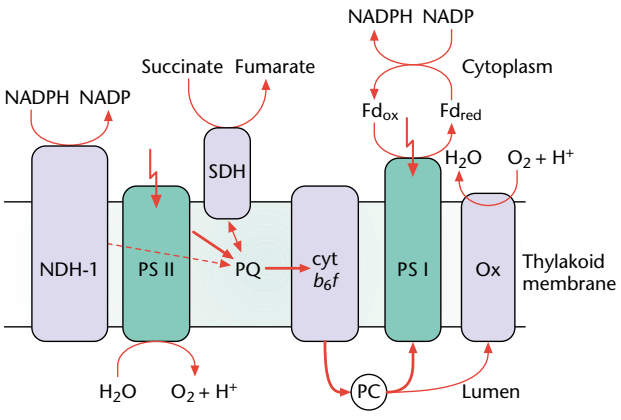

Figure 2 Schematic representation of the intersecting photosynthetic and respiratory electron transport pathways in thylakoid membranes of the cyanobacterium *Synechocystis* sp. PCC 6803. Arrows indicate electron transfer reactions, and thunderbolts designate light that sets into motion the redox reactions in the two photosystems. The thickness of each arrow is an approximate indication of the rate of the corresponding reaction. Electron transfer complexes that are specifically involved in photosynthetic electron transfer are PS II and PS I, whereas those specific for respiratory electron flow include NDH-1, SDH, and the terminal oxidase. PQ, cyt b_6f and PC are shared by both pathways. The electron transfer arrows involving SDH are drawn in both directions, as the difference in midpoint redox potentials between the PQ/PQH_2 and fumarate/succinate redox couples is small and therefore electron flow can occur in both directions depending on the relative concentrations of PQ, PQH_2, succinate and fumarate. *Abbreviations*: cyt b_6f, the cytochrome b_6f complex; Fd_{ox} and Fd_{red}, ferredoxin in oxidized and reduced forms, respectively; NADP(H), nicotinamide – adenine dinucleotide phosphate (reduced form); NDH-1, type 1 NADPH dehydrogenase; Ox, terminal oxidase; PC, plastocyanin; PQ, plastoquinone; PS I, photosystem I; PS II, photosystem II; SDH, succinate dehydrogenase.

for essentially opposite metabolic processes that occur at the same time does not appear to be a significant impediment in view of the stunning longevity with which cyanobacteria have been a major presence in life on earth.

A short overview of photosynthetic electron flow will be provided, followed by a summary of progress in the study of respiratory electron flow in cyanobacteria. In the last section, components involved in both photosynthesis and respiration in cyanobacteria will be covered.

Photosynthetic Electron Flow

The photosynthetic electron transport chain in cyanobacteria is essentially identical to that in plants, even though some of the polypeptides that are part of electron-transporting enzymes appear to be of different evolutionary origin in the two systems. Indeed, chloroplasts in plants are thought to have originated from cyanobacterial ancestors. The photosynthetic electron transport chain of oxygenic organisms has been reviewed extensively (for example, Ort and Yocum, 1996; Hippler *et al.*, 1998; Whitmarsh, 1998), so only a brief summary will be provided here. As indicated in **Figure 2**, photosystem II (PS II) uses light energy to split water and to reduce the PQ pool. **Table 1** summarizes the protein components involved with PS II and with other complexes mentioned in **Figure 2**. Electrons are transported from the PQ pool to the cytochrome b_6f complex and from there to a soluble electron carrier on the luminal side of the thylakoid membrane. In cyanobacteria this soluble carrier may be plastocyanin or cytochrome c_{553}, depending on the species and on the availability of copper (plastocyanin is a copper-containing enzyme). Either of these soluble one-electron carriers can reduce the oxidized PS I reaction centre chlorophyll, $P700^+$. This oxidized form of the reaction

Table 1 Major complexes involved with photosynthetic and respiratory electron flow in thylakoid membranes in cyanobacteria

Complex	Gene designation	Major proteins	Cofactors	Function
Photosystem II	*psb*	D1, D2, CP43, CP47, PsbO	Mn, Ca, Cl, Fe, PQ, chlorophyll, cyt b_{559}, pheophytin	Light-induced water splitting and PQ reduction
Succinate dehydrogenase	*sdh*	SdhA, SdhB, SdhC	Flavin, FeS centres	Succinate oxidation and PQ reduction
Type-1 NADPH dehydrogenase	*ndh*	NdhA-L	FeS centres	NADPH oxidation and PQ reduction
Cytochrome b_6f	*pet*	cyt b_6, cyt *f*, Rieske, subunit IV	2 cyt *b*, cyt *f* (cyt *c*), FeS	PQH_2 oxidation and PC/cyt c_{553} reduction
Photosystem I	*psa*	PsaA, PsaB and other Psa proteins	Chlorophyll, vitamin K_1, FeS centres	Light-induced PC/cyt c_{553} oxidation and Fd reduction
Cytochrome oxidase	*cta*	CtaC, CtaD, CtaE	Cu_A, Cu_B, Mg, cyt *a*, cyt a_3	Cyt *c* oxidation and O_2 reduction

centre chlorophyll is formed by a light-induced transfer of an electron from PS I to ferredoxin (Fd) and eventually to NADP. Reduced NADP can be used for CO_2 fixation.

Photosynthetic electron transfer leads to a proton gradient across the thylakoid membrane. In PS II, protons are released into the lumen upon water splitting, and protons formed upon plastoquinol oxidation by the cytochrome b_6f complex are released into the lumen as well. The proton gradient across the thylakoid membrane is used for ATP synthesis by the ATP synthase in the thylakoid; this ATP may be applied for CO_2 fixation and for other cell processes.

One important difference between cyanobacteria and plants is that the stoichiometry of PS I and PS II in at least some species of cyanobacteria is much larger than 1, whereas in higher plants an equal amount of PS I and PS II is the rule. For example, in the cyanobacterium *Synechocystis* sp. PCC 6803 the PS I/PS II ratio is about 5 (see Shen *et al*., 1993). One possible explanation for this unusual stoichiometry in cyanobacteria is the involvement of PS I in a significant amount of cyclic electron flow around this photosystem, in which electrons would flow from PS I/Fd back to PQ and cytochrome b_6f, and from there to PS I again (reviewed by Bendall and Manasse, 1995). This electron transport pathway should contribute to a proton gradient, which could be used for ATP synthesis, but would not lead to net NADP reduction. However, a high rate of cyclic electron flow around PS I in cyanobacteria cannot be demonstrated experimentally. Another and probably more plausible reason for the relatively large amount of PS I in cyanobacteria is the abundance of respiratory electron transfer pathways into the PQ pool, whereas the capacity of respiratory electron flow out of the PQ pool may be more limited (see the next section). Therefore, an abundance of PS I may guarantee a rather oxidized PQ pool in the light, which is important to minimize photodamage (reviewed by Andersson and Barber, 1996). Moreover, the high amount of PS I may serve to compete effectively with cytochrome oxidase for electrons when light is available, thus maximizing the number of electrons that can be used for CO_2 fixation.

Respiratory Electron Flow

The respiratory pathways in cyanobacteria have long been unclear or misunderstood. However, considerable insight has now been obtained in this important aspect of cyanobacterial physiology, primarily by making use of mutants lacking specific proteins. Much of this work has been performed on *Synechocystis* sp. PCC 6803, which is very amenable to targeted genetic modification (Vermaas, 1996) and which was the first cyanobacterium for which a complete genomic sequence has become available (Kaneko *et al*., 1996). It has now been realized that the main respiratory electron transport activity into the PQ pool in cyanobacterial thylakoids involves succinate dehydrogenase (SDH) activity rather than electron flow from NAD(P)H (Cooley *et al*., 2000); NADPH appears to be used preferentially for carbon fixation processes. The corollary of this new concept is that cyanobacteria are able to generate succinate as a respiratory intermediate, and therefore should have a (modified) citric acid cycle. According to the older literature, a citric acid cycle was presumed to be nonfunctional in cyanobacteria as a key enzyme, 2-oxoglutarate dehydrogenase, was absent (reviewed in Stanier and Cohen-Bazire, 1977). Indeed, this is true according to the genomic sequence of *Synechocystis* sp. PCC 6803, but this organism is able to convert 2-oxoglutarate to succinate in the absence of a traditional 2-oxoglutarate dehydrogenase complex (Cooley *et al*., 2000), making use of an alternate pathway.

NAD(P)H oxidation

The cyanobacterial equivalent of the mitochondrial and bacterial type-1 NADPH dehydrogenase (NDH-1) is an enzyme complex similar to the 14-subunit NDH-1 complex from *Escherichia coli*, except that three subunits involved with substrate binding are not apparent from the cyanobacterial genome. Probably related to this observation, the preferred substrate of cyanobacterial NDH-1 is NADPH rather than NADH. Upon inactivation of *ndhB*, the gene for one of the essential NDH-1 subunits, mutants required high CO_2 for growth (Ogawa, 1991) and showed a decreased respiration rate. The latter was taken to support the tacit assumption that NDH-1 was the major respiratory electron transport route into the PQ pool in cyanobacteria as it is in many other bacteria and in mitochondria from most eukaryotes. However, this view was challenged when mutants lacking succinate dehydrogenase activity showed a very slow rate of respiratory electron flow into the PQ pool (Cooley *et al*., 2000). As will be argued in a subsequent section, this suggests that NDH-1 activity in cyanobacteria *in vivo* is only very modest, and that most respiratory electrons enter the PQ pool via SDH. In cyanobacteria, NADPH is not used as a preferential respiratory substrate but rather is applied for the CO_2 fixation process. However, a large number (4–6) of isogenes for two of the NDH-1 subunits are present in the *Synechocystis* genome; these isogenes may have different functions (Ohkawa *et al*., 2000). This suggests that NDH-1 may function in different capacities depending on the physiological state of the cell.

According to the genomic sequence of *Synechocystis* sp. PCC 6803, this cyanobacterium is capable of producing type-2 NDH (NDH-2), which is a single-subunit protein and that may not contribute to a proton gradient over the thylakoid membrane. Three genes for NDH-2s are present in the *Synechocystis* sp. PCC 6803 genome, but so far no evidence has been found that would suggest a large activity

of NDH-2 in providing electrons to the PQ pool. Instead, NDH-2 in cyanobacteria may have a mostly regulatory function (Howitt *et al*., 1999).

Succinate dehydrogenase

Genes for soluble SDH subunits are easily identified in the *Synechocystis* sp. PCC 6803 genome, and upon deletion of such genes a phenotype consistent with a lack of SDH activity is found. Whereas fumarate (the SDH product) is depleted in mutants lacking SDH, succinate accumulates (Cooley *et al*., 2000). Moreover, in such mutants succinate accumulates to a higher degree when 2-oxoglutarate (an intermediate in the citric acid cycle before succinate) is added, signifying the capability of cyanobacteria to convert 2-oxoglutarate to succinate (Cooley *et al*., 2000) even though a traditional 2-oxoglutarate dehydrogenase is absent according to the genome sequence. This implies that cyanobacteria can utilize a modified citric acid cycle and that succinate and SDH are potentially important in cyanobacterial respiratory metabolism.

In the *Synechocystis* mutant lacking SDH activity, the rate of initial respiratory electron flow into the PQ pool was about an order of magnitude lower than in wild type, suggesting that essentially all respiratory electrons enter the PQ pool through SDH activity rather than through oxidation of NAD(P)H (Cooley *et al*., 2000). Therefore, the large effect of inactivation of *ndhB* (an NDH-1 gene; see above) on respiration may be an indirect effect due to the absence of succinate in this mutant: oxidized NAD(P) is needed for running the citric acid cycle and other respiratory processes. This highlights the complexity of metabolism even in rather simple organisms, and cautions against one-sided interpretations. However, the biochemical analysis of *Synechocystis* mutants specifically lacking particular subunits provides an opportunity to critically test previous and current hypotheses and interpretations.

Terminal oxidases

Using molecular-genetic approaches and the analysis of specific mutants, the nature and relative activity of terminal oxidases in *Synechocystis* sp. PCC 6803 has been clarified. According to biochemical data preceding the availability of the genomic sequence of this organism, a cytochrome aa_3-type cytochrome-*c* oxidase was found to be present along with another terminal oxidase (see Schmetterer (1994) for a review). According to the genome sequence, apart from a cytochrome-*c* oxidase there may be a cytochrome *bd*-type quinol oxidase as well as a second quinol oxidase that most resembles a cytochrome *bo*-type oxidase. The cytochrome *bd*-type quinol oxidase could be demonstrated on the basis of inhibitor studies as well as by mutant analysis, but the cytochrome *bo*-type oxidase does not appear to be expressed under the conditions used thus far. Interestingly, under the conditions used, the cytochrome *bd*-type quinol oxidase appears to be located predominantly in the cytoplasmic membrane, whereas significant cytochrome oxidase activity is seen in thylakoids (Howitt and Vermaas, 1998). Indeed, in mutants lacking PS I, rapid (40 ms) electron flow from PS II to cytochrome oxidase can be demonstrated, indicating a close functional relationship between PS II and thylakoid-localized cytochrome oxidase (Vermaas *et al*., 1994).

The presence of cytochrome oxidase in the cyanobacterial thylakoid membrane raises the question of what the electron donor may be. If cytochrome c_{553}, the luminal electron carrier that can replace plastocyanin, is present, then this is the likely electron donor. However, electron transfer to the oxidase can also occur in the absence of this cytochrome. This electron transfer appears to involve plastocyanin, but also seems to require another cytochrome, cytochrome c_M. This cytochrome *c* may serve as an electron transport intermediate and might be associated with the cytochrome oxidase complex (Manna and Vermaas, 1997). Limited sequence similarity exists between cytochrome c_M and the cytochrome *c*-binding part of the cytochrome caa_3-containing cytochrome-*c* oxidase from bacteria with such a complex, and cytochrome c_M appears to be required for electron flow out of the PQ pool under conditions that PS I and cytochrome c_{553} are absent (Manna and Vermaas, 1997).

Components Involved in Both Photosynthesis and Respiration

The plastoquinone pool

In *Synechocystis* sp. PCC 6803, apart from PQ the only quinone found in thylakoids is vitamin K_1 associated with PS I. Therefore, essentially all electron transport through unbound quinones appears to proceed via PQ in cyanobacterial thylakoids. Plastoquinone in the thylakoid membrane shuttles electrons from both photosynthetic and respiratory electron transport chains to the cytochrome b_6f complex. PQ is reduced to the quinol form by accepting two reducing equivalents, but, when bound to protein, the semiquinone form (the radical form with one electron more than the quinone and one electron less than the quinol) can be stabilized. Therefore, PQ can function as an adapter converting one-electron redox reactions (as they occur, for example, in PS II and cytochrome b_6f) to two-electron reactions and vice versa.

The cytochrome b_6f complex

A key complex in both photosynthetic and respiratory electron transfer in cyanobacteria is the cytochrome b_6f complex. Efforts to fully inactivate this complex in cyanobacteria have been unsuccessful thus far, indicating

the central role this complex plays in electron transport. Indeed, all electron transfer in photosynthesis and respiration, with the exception of respiratory electron flow to quinol oxidases, needs to proceed through the cytochrome b_6f complex. However, as quinol oxidase may not be prevalent in thylakoids under many growth conditions and may occur predominantly in cytoplasmic membranes (Howitt and Vermaas, 1998), essentially all plastoquinol oxidation in thylakoids occurs via the cytochrome b_6f complex in wild type under most growth conditions.

The redox-active components of the cytochrome b_6f complex are associated with the cytochrome b_6 apoprotein, the cytochrome *f* apoprotein, and the Rieske FeS centre. A fourth major component, subunit IV, does not carry redox-active cofactors. In mitochondria and Gram-negative bacteria containing a bc_1 complex, cytochrome b_6 and subunit IV are fused. Another interesting feature when comparing cytochrome b_6f and cytochrome bc_1 complexes is that cytochrome *f* and cytochrome c_1 do not have a common ancestor, in spite of their homologous function. In line with the different origins of the two cytochromes, in cytochrome *f* the N-terminal amino group of the processed protein forms a covalent bond with the haem group, whereas this is not the case for cytochrome c_1.

Perhaps the cyanobacterial mutant generated thus far with the lowest amount of cytochrome b_6f activity is one where *ccs*B, a gene coding for a protein involved in maturation of cytochrome *f*, has been impaired (Tichy and Vermaas, 1999). This mutant contains an N-terminally modified CcsB that stabilizes preapocytochrome *f* but that is inefficient in maturation of the cytochrome (N-terminal processing and covalent attachment of the haem). Consequently, the *ccsB* mutant accumulates preapocytochrome *f* and has about a 5-fold reduced amount of mature, functional cytochrome b_6f. This strain grows only microaerobically, and partial restoration of CcsB function also restores the ability to grow aerobically. The role of oxygen remains to be elucidated, but it may involve regulation of gene expression.

An interesting feature of the cyanobacterial cytochrome b_6f complex is that in the *Synechocystis* sp. PCC 6803 genome three genes are found that may code for Rieske FeS centres, whereas only a single set of genes is present for the other components of the complex. One possible reason for this unexpected complexity is that the different Rieske FeS centres differ in their interaction of the cytochrome b_6f complex with soluble carriers, thus providing a mechanism for regulation of electron flow to PS I versus to the terminal cytochrome oxidase.

Soluble electron carriers

Both plastocyanin and cytochrome c_{553} can function in both photosynthesis and respiratory electron transport. In mutants lacking PS I, the gene for either soluble redox carrier can be deleted with only a moderate effect on the rate of electron flow from PS II via the quinone pool, the cytochrome b_6f complex and the remaining soluble carrier to the cytochrome aa_3-type cytochrome oxidase. In mutants lacking either plastocyanin or cytochrome c_{553}, photosynthetic electron transport rates remain normal, indicating that either of the two soluble carriers is sufficient.

Interestingly, efforts to delete the genes for both plastocyanin and cytochrome c_{553} in the same strain have been unsuccessful, indicating that one of the two carriers is required to shuttle electrons to PS I and cytochrome oxidase.

Regulation of Photosynthesis and Respiration

A central question that will now need to be addressed is how photosynthesis and respiration are regulated in a cyanobacterium. For regulation, an important issue is the capacity and rate of the various steps. The approximate capacities of electron transfer steps in *Synechocystis* sp. PCC 6803 are summarized in **Table 2**. The actual rate of the reactions may be significantly lower *in vivo*, depending on the conditions (light intensity, redox state, etc.). From **Table 2**, it is clear that PS I activity is abundant relative to that of the cytochrome b_6f complex, and this may explain in part the slow $P700^+$ rereduction kinetics (100–200 ms half-time) that are generally observed after a period of illumination. If light is abundant, the photosynthetic electron transport chain has a much higher capacity of electron flow than has the respiratory chain, but at very low light intensity or in darkness respiratory rates are higher than those of photosynthesis. As the capacities of cytochrome oxidase and succinate dehydrogenase seem comparable, respiratory electron flow will not lead to major changes in the redox state of the PQ pool (over-reduction or overoxidation), leaving room for regulation of metabolic processes that are apparently mediated via the PQ redox state.

Parallels to the Situation in Chloroplasts

An important question is that of the relevance of the insights obtained thus far on *Synechocystis* for electron transport events in other organisms, such as plants. In photosynthetic eukaryotes, photosynthetic and respiratory electron flows have been separated as they occur in two different organelles. However, chloroplasts retain

Table 2 Approximate capacity and probable source of rate limitation of photosynthetic and respiratory electron transfer in *Synechocystis* sp. PCC 6803. (For simplicity, these values have been expressed on a per-chlorophyll basis)

Complex	Capacity (μmol electrons h^{-1} per mg chlorophyll)	Source of rate limitation
Photosystem II	1000	Light intensity, availability of oxidized PQ
Succinate dehydrogenase	200	Succinate concentration, PQ pool redox state
NADPH dehydrogenase	20	NADPH availability, PQ pool redox state
Cytochrome b_6f complex	1000	PQH_2 concentration
Photosystem I	3000	Light intensity, Fd/NADP availability, reduced cyt c_{553}/PC
Cytochrome-*c* oxidase	200	Reduced cyt c_{553}/PC availability

certain cyanobacterial features involved in respiratory electron flow. For example, genes for the NDH-1 complex are retained in the chloroplast genome, and a small amount of NDH-1 activity can be demonstrated (Burrows *et al*., 1998). However, there is little evidence for significant activity of SDH or of a terminal oxidase in chloroplasts under normal conditions. None the less, the case for respiratory activity in chloroplasts ('chlororespiration') is slowly building, even though it may not involve the same components that are prevalent in cyanobacteria (for example, Cournac *et al*., 2000). However, it is likely that comparisons with the cyanobacterial system will further guide the search for components involved in such activities in chloroplasts.

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