Proc. Natl. Acad. Sci. USA
Vol. 75, No. 4, pp. 1801–1804, April 1978
Botany

Photosynthetic characteristics and organization of chlorophyll in marine dinoflagellates

(photosynthesis/chlorophyll–proteins/photosynthetic unit/algae/light-harvesting)

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Communicated by Paul J. Kramer, February 2, 1978

ABSTRACT The photosystem I reaction center complex, the *P*-700–chlorophyll *a*-protein, has been isolated from the photosynthetic membranes of two marine dinoflagellates, *Gonyaulax polyedra* and *Glenodinium* sp., by detergent solubilization with Triton X-100. The complexes isolated from the two species were indistinguishable, exhibiting identical absorption properties (400–700 nm) at both room (300 K) and low (77 K) temperature. The room temperature, red wavelength maximum was at 675 nm. The absorption properties, kinetics of photobleaching, sodium dodecyl sulfate electrophoretic mobilities, and chlorophyll *a*/*P*-700 ratio (50 ± 10) of the *P*-700–chlorophyll *a*-protein complexes from the two species also were essentially the same and similar to those properties characterizing *P*-700–chlorophyll *a*-protein complexes of higher plants and green algae.

Photosynthetic unit sizes were determined for cells grown at 1000 $\mu W/cm^2$. Both dinoflagellates had unit sizes (total chlorophyll/*P*-700 ratios) of about 600, even though the distribution of chlorophyll *a*, chlorophyll *c*, and peridinin in the light-harvesting components differed in *Gonyaulax* and *Glenodinium*. The number of photosynthetic units per cell in the two species correlates directly with their photosynthetic activities. A model is presented for the distribution of chlorophyll in the photosynthetic apparatus of these dinoflagellates which accounts for the known role of the isolated pigment–protein complexes and for the known photoadaptive physiology in pigmentation and photosynthesis for these species.

Among the major primary producers in the sea, photosynthetic dinoflagellates are often found growing in light-limited environments (1–4). Members of this group succeed as major components of periodic blooms of photoplankton in coastal areas and estuaries, as endosymbionts in a variety of marine organisms, as vertical migrants through the photic zone, and as deep free-living inhabitants in the ocean. Much of the success of these dinoflagellates may be attributed to their photoadaptive capabilities, especially the flexibility of their photosynthetic pigment system which adjusts to changes in environmental light levels. Therefore, the present study sought to further investigate the photoadaptive ability of two dinoflagellate species, *Glenodinium* sp. and *Gonyaulax polyedra* by considering their known physiological and growth characteristics and by examining the *in vivo* organization of chlorophyll in the photosynthetic apparatus.

Both *Glenodinium* and *Gonyaulax* are armored and polyhedral and, typical of dinoflagellates, both contain brown chloroplasts heavily pigmented with chlorophyll (Chl) *a*, Chl *c*, and the carotenoid, peridinin. *Gonyaulax* is larger than *Glenodinium* and is well known for its involvement in red tides. Growth is saturated at a relatively low light intensity (1000 $\mu W/cm^2$) for both species (1, 2). In addition, *Glenodinium* and *Gonyaulax* exhibit circadian rhythms of oxygen evolution unrelated to pigmentation (3) and undergo photosynthetic photoadaptive responses characterized by increased pigmentation and a maintenance of photosynthetic capacity at lower light levels (1, 2).

In the present study we asked specifically how is chlorophyll functionally organized in the photosynthetic unit in these algae and is this organization related to the ability of these dinoflagellates to light-adapt, to grow, and to carry out adequate rates of photosynthesis. From the data obtained on known Chl *a*-protein complexes that were isolated from *Gonyaulax* and *Glenodinium*, combined with physiological data and biochemical information on the existence of other pigment–protein complexes, a working model is proposed for the organization of chlorophyll in the light-harvesting and reaction center components of these dinoflagellates.

MATERIALS AND METHODS

Algal Culture. Culture conditions for *Glenodinium* sp. (L. Provasoli, M. Bernard strain; UCSB code no. 5M29) and *Gonyaulax polyedra* Stein clone 70A (UCSB code no. 5M19) have been described (3). Cells were grown on a 12-hr light 12-hr dark schedule at 20 ± 2°C. Overhead illumination was provided by banks of cool-white fluorescent lamps with irradiances of 800–1000 $\mu W/cm^2$. Cells in late exponential phase of growth were collected by centrifugation (4000 × *g* for 10 min). They were resuspended in a small volume of 50 mM Tris·HCl, pH 8.0, and stored frozen.

Preparation of Chloroplast Lamellae. Algal cells were broken in 50 mM Tris-borate buffer containing 5 mM $MgCl_2$ either by sonication or by two passes through a French pressure cell at 16,000 lbs./inch^2. The cellular debris and unbroken cells were removed by centrifugation at 3000 × *g* for 5 min. The supernatant, which contained photosynthetic lamellae, was then washed three times in 50 mM Tris-borate (pH 8.0) containing 4 mM $MgCl_2$ by centrifugation at 40,000 × *g* for 10 min and resuspension with a Kontes glass homogenizer. For *Glenodinium*, it was necessary to wash the membranes twice more to remove as much of the peridinin–Chl *a*-protein complex (PCP) as possible (4).

Preparation of Lamellae Detergent Extracts. The well-washed lamellae of *Glenodinium* and *Gonyaulax* were solubilized in either 1% Triton X-100 (Triton/Chl *a* = 75/1, wt/wt) by the procedures outlined in Shiozawa *et al.* (5) or in 1% sodium dodecyl sulfate ($NaDodSO_4$) ($NaDodSO_4$/Chl *a* = 10/1, wt/wt) (6, 7). The Triton-solubilized lamellae were used for the isolation of *P*-700–Chl *a*-protein by hydroxylapatite chromatography. The $NaDodSO_4$ extracts were used for analysis of the pigment–protein complexes by $NaDodSO_4$/polyacrylamide gel electrophoresis. The electrophoresis system consisted of 7.5%

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Abbreviations: Chl, chlorophyll; $NaDodSO_4$, sodium dodecyl sulfate; PCP, peridinin–chlorophyll *a*-protein; PSU, photosynthetic unit(s).

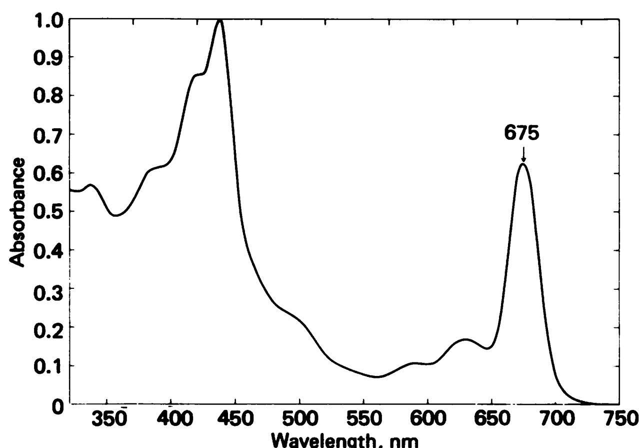

FIG. 1. Room temperature (300 K) absorption spectrum of the *P*-700–Chl *a*–protein isolated from *Glenodinium* sp.

acrylamide gels containing 0.05% $NaDodSO_4$, 4 mM $MgCl_2$, and 50 mM Tris·HCl (pH, 8.0) (final concentrations). The running buffer was identical to the gel buffer. Approximately 20–30 μl of $NaDodSO_4$ extract was loaded on gel columns (0.8 × 14 cm) that had been pre-electrophoresed. The samples were electrophoresed at about 10 mA/tube (at a constant voltage of 110 V) for 20–40 min. After this time, complex I, the $NaDodSO_4$-altered form of the *P*-700–Chl *a*–protein (7), and other pigment zones (7–9) were distinguished.

Spectrophotometric Analyses. The amount of *P*-700 was estimated from light-oxidized and dark-reduced difference spectra of Triton extracts and of isolated *P*-700–Chl *a*–protein on an Aminco DW-2 dual beam spectrophotometer (5). Low-temperature spectra (77 K) of whole cells, lamellae, and *P*-700–Chl *a*–protein were also determined.

RESULTS

When spectra, either room temperature or 77 K, of whole cells of *Glenodinium* and *Gonyaulax* are compared, no significant differences in absorption properties from 400 to 700 nm are observed (ref. 10 and unpublished results). Likewise, comparison of either the 77 K or the 300 K absorption spectra of the *P*-700–Chl *a*–protein isolated from these two species are essentially the same and indistinguishable from absorption properties observed for the complex isolated from higher plants and green algae (5, 7) (Fig. 1). The red wavelength maximum for the complex isolated from both species was 675 nm. The wavelength of maximum light-induced bleaching of *P*-700 in Triton extracts of lamellae and in the *P*-700–Chl *a*–protein was at 697 nm, in agreement with findings on yellow-green, blue-green, and golden-brown algae (7). The kinetics of light-oxidation and dark-reduction of *P*-700 were rapid but readily enhanced with a sodium ascorbate/methyl viologen couple as were those previously described (5, 7). The isolated *P*-700–Chl *a*–protein of both species had a Chl *a* to *P*-700 ratio of 50 ± 10; an average of six determinations for each species (Table 1).

$NaDodSO_4$-solubilized lamellae of both species yielded upon electrophoresis a characteristic blue-green band of slowest electrophoretic mobility. This pigmented zone electrophoresed coincident with complex I, the $NaDodSO_4$-altered form of the *P*-700–Chl *a*–protein of the blue-green alga *Phormidium luridum* (5, 8). Two additional pigment bands were observed consistently, one of intermediate mobility, which represented the bulk of the pigment and was orange-brown, and one of greatest mobility, which was orange-yellow. Only the pigmented zones of the slowest (complex I) and intermediate mobility stained for protein. It is likely that the intermediate zone on the gel contains principally chlorophyll- and carotenoid-binding proteins, whereas the fastest migrating zone probably represents only pigment that has been released from its native protein moieties by the action of the detergent (8). That this is the case is confirmed by preliminary spectral analysis of the pigment zones. The zone of intermediate mobility was rich in Chl *c* and contained peridinin in addition to Chl *a*. The zone with free pigment principally contained Chl *a* in addition to peridinin and an unidentified carotenoid. No Chl *c* was detected in this gel zone. These observations suggest that Chl *a* and Chl *c* either are associated with very similar proteins or are in fact associated with the same protein.

Table 1. Photosynthetic and cell characteristics of *Gonyaulax* and *Glenodinium* grown on a 12-hr light 12-hr dark schedule at 1000 $\mu W/cm^2$

Parameter*	*Gonyaulax*†	*Glenodinium*‡
Cell size (μm)	60 × 40	16 × 11
Chl *a* (μM per cell)	750×10^{-10}	14×10^{-10}
Chl *a*/Chl *c*§	1.7	1.6
Peridinin/Chl *a*§	1.25	2.0
Photosynthetic rate		
(μM O_2/cell per hr)	1500×10^{-8}	35×10^{-8}
(μM O_2/μM Chl *a* per hr)	200	250
PSU‖ size		
(total Chl *a*/*P*-700)	600 ± 10	600 ± 10
No. of PSU/cell‖		
(nM *P*-700/cell)	1.25×10^{-10}	0.023×10^{-10}
Chl *a*/*P*-700 in		
P-700–Chl *a*–protein	50 ± 10	55 ± 10

* Average of at least three determinations.
† Pigmentation and photosynthetic rates from ref. 2.
‡ Pigmentation and photosynthetic rates from Prézelin *et al.* (3).
§ Molar ratio.
‖ Photosynthetic unit.

The ratio of total chlorophyll to *P*-700 (PSU size) in Triton extracts of *Glenodinium* and *Gonyaulax* grown at 1000 $\mu W/cm^2$ both were approximately 600:1 (see Table 1). That the PSU size is about the same when the two algae are cultured under similar conditions would suggest that light saturation of photosynthesis in these species should occur at the same light intensity. Independent measurements of photosynthetic light saturation showed this to be the case (1, 2). A PSU size of about 600 is similar to that obtained previously for a golden-brown alga (7) and more recently (M. J. Perry and R. S. Alberte, unpublished data) for a diatom species.

Based on an average PSU size of 600 and a determination of the cellular Chl *a* content, it was possible to calculate the number of PSU per cell (11). In this calculation we assumed that each PSU contained one *P*-700 molecule and that every unit was the same size (12). The number of PSU per cell is 50-fold greater in *Gonyaulax* than in *Glenodinium* (Table 1). Such a situation would be anticipated since *Gonyaulax* is larger, contains 50 times more Chl *a*/cell, and has a light-saturated cellular photosynthetic rate almost 50-fold greater than *Glenodinium* (Table 1). Previous reports (6, 11, 13) have established a strong correlation between the number of PSU and light-saturated photosynthetic activity in higher plants (when expressed as CO_2 exchange per unit leaf area). This same relationship has been established in these two marine dinoflagellates.

DISCUSSION

Gonyaulax and *Glenodinium* are two important phytoplankton species which contribute to the primary productivity of the oceans. They are distinct in many characteristics from the green and other algal classes of photoplankton in that they possess a unique light-harvesting pigment–protein complex called PCP.

This complex is made up of the carotenoid, peridinin, and Chl *a* in a molar ratio of 4 to 1 (4, 14). PCP is the principal light-harvesting component in the photosynthetic apparatus of these organisms and, at low light levels, accounts for about 50% of the total Chl *a* in *Glenodinium* and 30% of the Chl *a* in *Gonyaulax*. That this complex fulfills its role as the major light-harvesting component is shown by its efficient light capture and energy transfer ability, depicted in action spectra for O_2 evolution for whole cells, and in fluorescence excitation spectra for isolated PCP (4, 14).

In light adaptation studies (1, 2) it has been demonstrated clearly that the amount of PCP present in these two dinoflagellates is directly related to the light intensity under which the cells grow. *Glenodinium* grown under low light intensity (250 $\mu W/cm^2$) has a greater proportion of its total Chl *a* localized in this complex, hence providing a larger light-gathering capacity (10). Similarly, *Gonyaulax* cells also contain increased amounts of PCP when cultured at lower light levels, but the proportion of total Chl *a* in PCP remains constant at about 30–40%. This is presumably due to a concomitant increase in the concentration of another light-harvesting component containing both Chl *a* and Chl *c* (2).

In green plants it has been shown (7, 11–13, ‡) that the Chl *a/b*–protein serves as the principal light-harvesting component in the PSU; this same function has been demonstrated recently for PCP. The amount of the Chl *a/b*–protein also varies in response to light intensity, accounting for changes in total Chl as great as 30–40% and for the changes in the PSU size (7, 12, ‡); the lower the environmental light level, the greater the amount of the light-harvesting complex, and the larger the PSU size. This same relationship holds true for the dinoflagellates. When the cellular content of PCP changes due to changes in light intensity, there are consequent and parallel changes in the PSU size. Therefore, because of the many similarities between the light-harvesting system of dinoflagellates and green plants, we sought to evaluate the *in vivo* distribution of chlorophyll in the PSU of these algae, and propose a working model for the organization of their chlorophyll-containing components as was done previously for green plants (12).

As shown in the present study, both *Glenodinium* and *Gonyaulax* contain the *P*-700–Chl *a*–protein which had been proposed (7) to be ubiquitous in the photosynthetic plant kingdom. This complex typically contains 40 Chl *a* molecules and *P*-700 (4). For our purposes here, we have allocated 40 of the 600 chlorophyll molecules in the PSU to this complex, inasmuch as the values for the isolated complex from *Glenodinium* and *Gonyaulax* are not significantly higher (Table 2). Twenty Chl *a* molecules have been attributed to the reaction center of photosystem II as described in the green plant model (12). Hence, the two reaction center entities account for 10% of the total Chl *a* in these dinoflagellates. About 120 Chl *a* molecules have been allocated to the proposed (8, 12) light-harvesting Chl *a*–protein complex, as described for the green plant PSU (12). That this component accounts for about this proportion of the total Chl *a* has been determined by the common occurrence of about 120 Chl *a* molecules not accounted for by the known Chl–protein complexes in the PSU of two species of red algae (*Griffithsia* and *Porphyra*) (unpublished data), cyanobacteria (7, 8, 12, 16, 17, ‡), and green plants (8, 12). This component, in conjunction with the reaction center complexes, accounts for 180 Chl *a* molecules, in agreement with the value determined experimentally for the PSU (Chl *a*/*P*-700) of blue-green and red algae (8, 12, 17, ‡) which have no chlorophyll in their major light-harvesting system; the

‡ R. S. Alberte and J. P. Thornber, unpublished data.

Table 2. Proposed distribution of chlorophyll in the PSU of *Gonyaulax* and *Glenodinium* grown on a 12-hr light 12-hr dark schedule at 1000 $\mu W/cm^2$*

	Gonyaulax		*Glenodinium*	
	No. of Chls	% of total Chl	No. of Chls	% of total Chl
P-700–Chl *a*–protein	40	10	40	10
PS_{II} reaction center†	20		20	
LH Chl *a*–protein‡	120	20	120	20
Chl *a/c*–protein	240	40	120	20
PCP	180	30	300	50
Total	600	100	600	100

PSU size = 600.
* See text for explanation.
† PS_{II}, photosystem II.
‡ LH, light-harvesting.

phycobilipigments replace chlorophyll as light-harvesting pigments (15). The amount of Chl *a* in this common chlorophyll core appears not to be affected by changes in environmental light intensities (refs. 16, 17, ‡).

It has been determined experimentally (14) from the amount of water-soluble or lipid-associated PCP, that there are four peridinin molecules for each Chl *a* and that there is no Chl *c* associated with the PCP complex. In whole cells of *Gonyaulax* there is only 1.25 times as much peridinin as Chl *a*, whereas in *Glenodinium* there is 2.0 times as much (Table 1). Therefore, in *Gonyaulax* the total Chl *a* contributed by PCP is 60% that contributed in *Glenodinium*, or 180 Chl *a* molecules in the former and 300 in the latter (Table 2). When expressed as a percent, 30 and 50% of the total Chl *a* is contributed by PCP to the PSU in *Gonyaulax* and *Glenodinium*, respectively.

The existence of a Chl *a/c*–pigment complex has not been unequivocally demonstrated; however, its presence is suggested from several lines of evidence: first, all of the peridinin in these dinoflagellates appears to be associated with Chl *a* and not Chl *c* (2); second, not all of the cellular Chl *a* can be accounted for by the before-mentioned components (e.g., the reaction center, light-harvesting Chl *a*, and PCP complexes); third, during photoadaptation of *Gonyaulax* to decreasing light intensity from 3000 to 1700 $\mu W/cm^2$, an increase in PCP only accounts for 25–35% of the increase in total cellular Chl *a*, but accounts for all of the increase in peridinin (2); fourth, under these light adaptation conditions, the cellular content of Chl *c* in *Gonyaulax* increases proportionately to the non-PCP Chl *a*; fifth, there is evidence (18) that a Chl *a/c* complex exists in the brown algae; and sixth, in the present study we observed that Chl *a* and Chl *c* are found together in a pigment–protein zone on $NaDodSO_4$/polyacrylamide gel electrophoresis. Therefore, it is reasoned that the Chl *c* increase is directly related to the increase in non-PCP-associated Chl *a* and that it is likely that Chl *a* and *c* exist together *in vivo* as a distinct pigment–protein complex. If such is the case, it can then be calculated that the proposed Chl *a/c* complex would account for 40% of the chlorophyll in *Gonyaulax* and only 20% in *Glenodinium* at 1000 $\mu W/cm^2$. Important to note here is that despite the fact that the distribution of chlorophyll between PCP and a Chl *a/c* complex in the two species is not the same, the percent of the total chlorophyll in the bulk light-harvesting system for the two species is identical (70% of the total chlorophyll).

Based on the described distribution of chlorophyll in reaction center and light-harvesting components of these dinoflagellates, we have proposed a working model for the organization of these components into a functional PSU (Fig. 2). This working model

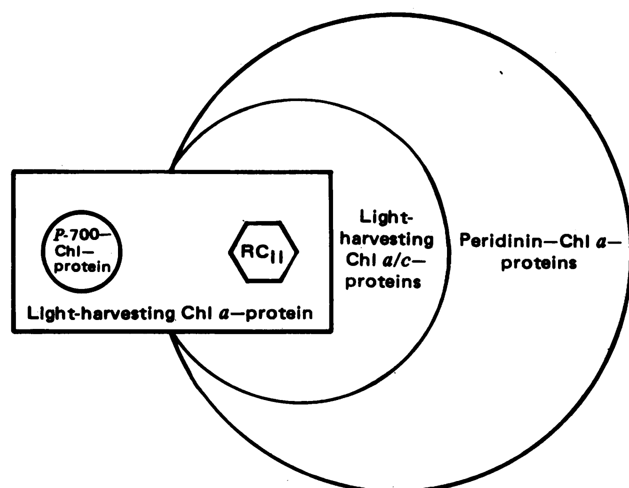

FIG. 2. A model depicting the distribution of chlorophyll in the photosynthetic unit of dinoflagellates. The proportions of the light-harvesting components shown approximate the chlorophyll distribution in the PSU of *Glenodinium* sp. (see Table 2 and text). However, the proportions of these components could be varied to meet the determined amounts of the respective chlorophyll–protein complexes in other species. RC_{II}, photosystem II reaction center.

has several appealing characteristics which are supported by physiological, spectral, and biochemical data. The central rectangular portion of the model is identical to that proposed earlier by Thornber *et al.* (12) as the common chlorophyll core for photosynthetic Chl *a*-containing organisms. Whereas the bulk light-harvesting system in green plants is composed of the Chl *a/b*-protein, in the dinoflagellates, PCP and the proposed Chl *a/c* complex effectively serve this function, as demonstrated by action spectra for photosynthesis (10, 15). In other algal classes, other light-harvesting systems function—for example, the phycobilipigments in the blue-green and red algae (15, 19).

As demonstrated by Prézelin (1), *Glenodinium* appears to use only PCP as an adaptive strategy for light acclimation whereas *Gonyaulax* uses both PCP and a Chl *a/c* system (2). Based on our proposed distribution of chlorophyll in the PSU, PCP is the most external component and hence the most easily removed or added both physiologically and experimentally. In this respect the protein moieties of PCP are predominantly hydrophilic, surrounding the chromophore which lies in a hydrophobic crevice (2). In addition, they contain a larger number of polar amino acids (4, 20) than reported for known membrane-bound Chl *a*–protein complexes (8, 12). In fact, in *Glenodinium* and other PCP-containing dinoflagellates, PCP is water soluble and is readily removed experimentally from the cells without addition of detergent (10, 21). Further, with such an organization it would be expected, on a physiological basis, that in *Glenodinium* the bulk of the change in light-harvesting capacity in response to light intensity should be mediated through PCP, which is precisely the case (1). However, in *Gonyaulax*, PCP accounts for only 30% of the total Chl *a*. In order to allow for the same degree of light acclimation as seen in *Glenodinium*, a sizable change in a Chl *a/c* component would be expected. Based on our model, we would anticipate that, during light adaptation in *Gonyaulax*, changes in PCP should be paralleled by changes in a Chl *a/c* component. This is exactly what has been observed (2). Therefore, in order to achieve a similar reduction in PSU size in response to high light intensity, for example, to account for a 50% reduction in cellular Chl *a*, *Gonyaulax* would have to lose all of its PCP plus a portion of its Chl *a/c* component whereas *Glenodinium* would need to lose only its PCP. For these physiological reasons, and because the Chl *c* in these organisms is not readily removed from the cells except with the addition of detergent, we feel that a Chl *a/c* component would be in close association with the known (12) hydrophobic Chl *a*–protein components depicted in the central rectangle of the model (Fig. 2).

Thus, the proposed model provides an explanation for the distribution of chlorophyll in the photosynthetic apparatus of dinoflagellates which accounts for the known role of isolated Chl–protein complexes and the photoadaptive physiology observed in their pigmentation and photosynthesis. The present description of the PSU should provide not only a useful framework for future studies aimed at interpreting the adaptive physiology underlying the growth and ecology of these dinoflagellates, but also should provide information valuable to efforts aimed at obtaining a complete picture of the organization of chlorophyll *in vivo*.

We acknowledge the helpful suggestions and discussions with Drs. B. M. Sweeney (Univ. of Calif., Santa Barbara) and J. P. Thornber (Univ. of Calif., Los Angeles). B.B.P. was supported by National Science Foundation Grant BMS 72-03331403 (awarded to B. M. Sweeney) and OCE-76-13919 (awarded to B.B.P.) and R.S.A. was supported in part by National Science Foundation Grant PMC 72-20252 (awarded to J. P. Thornber), National Science Foundation-Energy-related and National Institutes of Health fellowships, The Louis Block Foundation and Sprague Memorial Institute at the University of Chicago, and a U.S. Department of Agriculture–Agricultural Research Service Cooperative Agreement.

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