AGRICULTURAL BIOLOGY,
2017, V. 52, № 5, pp. 843-855
(SEL'SKOKHOZYAISTVENNAYA BIOLOGIYA)

ISSN 2412-0324 (English ed. Online)
ISSN 0131-6397 (Russian ed. Print)
ISSN 2313-4836 (Russian ed. Online)

Future agriculture systems

UDC 631.522/.524:581.132.1:57.05

doi: 10.15389/agrobiology.2017.5.843rus
doi: 10.15389/agrobiology.2017.5.843eng

CHLOROPHYLL b AS A SOURCE OF SIGNALS STEERING PLANT DEVELOPMENT

(review)

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The authors declare no conflict of interests
Acknowledgements:
Supported by Russian Science Foundation (grant № 14-16-00120)
Received December 12, 2016

Abstract

Crop yield strongly depends on time of the onset of flowering as well as of the initiation of senescence. These processes are under tight control of multiple gene complexes. Suboptimal environmental conditions, as well as mutations, may cause changes in the expression levels of these genes, which, in turn, can result in a delay of flowering and/or early senescence, and, ultimately, in a decrease of yield. Recently, crucial role in the regulation of plant development via retrograde signaling pathways has been revealed for chlorophyll b. Chlorophyll b is an obligate component of the photosynthetic apparatus of land plants, and the main regulator of the biosynthesis and degradation of photosynthetic antennae. It is becoming clear that the size and stability of photosynthetic antennae are not only important for photosynthesis but also represents a source of signaling beyond chloroplasts. The absence of chlorophyll b in mutants of *Arabidopsis thaliana* (*ch1*) and *Hordeum vulgare* (*chlorina f2 3613*) leads to a decrease in the growth rate, leaf size and biomass production. In addition, and independently of the downregulation of photosynthesis, the lack of chlorophyll b results in the delay of flowering and early onset of ontogenetic as well as induced senescence. This review addresses the role of chlorophyll b in energy balance, and discusses new data on the role of chlorophyll *b* in regulation of ontogenesis not related to photosynthesis. Mutants of economically important crops impaired in chlorophyll b biosynthesis represent promising models for physiological, biochemical and molecular studies of regulation of flowering and senescence, as the results can be directly applied to agricultural practice. Also, we review the novel data on the potential importance of plants with truncated photosynthetic antenna for increase in vegetative and grain biomass production. A decrease in chlorophyll b contents and the following down-regulation of antenna proteins were shown to influence the rate of electron transport within the photosystem II, as well as the rate of CO_2 assimilation relative to chlorophyll unit. Strikingly, these parameters in *chlorina* mutants are higher than in wild type plants by 15-20 %. Using plants with this type of photosynthetic apparatus can potentially bring about a considerable increase in yield. This suggestion has been recently supported by data on transgenic tobacco plants with truncated photosynthetic antenna (H. Kirst et al. 2017). At the same time, the consequences of the decrease in chlorophyll b levels for ontogenetic regulation and photoprotection typically negate the potential benefit of the acceleration of the limiting factor of photosynthesis, the photosystem II. This review discuss the possible ways to search for optimization of plant functions regulated by chlorophyll b, to provide new mechanisms of the increase in photosynthesis and crop production in agriculture.

Keywords: yield, chlorophyll b, flowering, ontogenesis, senescence, photosynthetic antenna

The yield of cereals depends on many factors. In addition to environmental conditions (availability of necessary nutrients, light, soil moisture, etc.), it is affected by endogenous processes. For example, violation of the expression of several regulatory genes can result in delayed flowering and accelerated senescence [1-2]. It is obvious that such changes in ontogenesis adversely affect yield.

Even a slight delay in the initiation of floral transformation of the vegetative apical meristems of shoots can lead to a substantial reduction in harvest, and at the shift of ontogenesis phases in time, the negative impact of environmental factors on the plant growth and yield dramatically increases. Blocking of transition to flowering leads to a complete loss of the grain harvest, as the spikes (with accelerated senescence they cannot be formed) are of agricultural value for these crops. At the same time, the acceleration of start of floral transformation of vegetative meristems even by 2-3 days (for example, early flowering barley and wheat mutants) [3] has a positive impact on productivity. Searching for such mutants and their introduction into the culture are actively carried out in the largest center for the study of barley – the Carlsberg Research Centre (Denmark).

Currently, there are a large number of mechanisms governing the change of ontogenesis phases [1, 4-6]. It is well known that for the timely passage of plants from one ontogenesis phase to another one, the availability of nitrogen and carbon is important [5]. For many cultures, it is established that the transition to flowering is initiated at a high ratio of far-red light to the red in the spectrum [7]. The most important factors regulating flowering are the length of daylight and temperature [8]: the cold pathway is stimulated at specific exposure to low temperatures (vernalization), and the photoperiodic one is triggered by a certain length of daylight [9]. Gibberellic signaling and the so-called autonomous induction of flowering also refer to the major signaling pathways that initiate flowering [4]. The structural and molecular genetic mechanisms of flower formation in response to floral transformation of the vegetative apical meristems of a stem have been studied [10-13].

The process of plant senescence is of key importance in the formation of crop yield [14, 15]. Senescence is the terminal stage of the development of tissue, organ or a whole plant [16], a genetically determined and an integral part of ontogenesis [17-19]. In early induction caused by adverse environmental conditions, senescence can result in a decrease of yield of vegetable and fodder crops [20, 21]. In most cases, the decay of leaves is consistent with the development of seeds, apical leaves and storage organs [22, 23], since the primary purpose of senescence is the remobilization of nutrients to plant young parts and seeds [24, 25]. For annuals, which include most cereal crops, the transport of nutrients from vegetative tissues into seeds during the senile stage is crucial: over 70 % of nitrogen is supplied to seeds from senescent leaves [14, 26-28]. Like flowering, senescence depends on the expression of regulator genes [27-29], which act both as activators and transcriptional repressors of target genes [30-33].

Previously, the biosynthesis of photosynthetic pigments, in particular, chlorophylls, was not considered a factor activating signaling pathways that lead to the initiation or a delay of flowering and senescence. However, recent works show the importance of the auxiliary photosynthetic pigment chlorophyll b (Chlb) in the regulation of plant ontogenesis. Chlb overproduction in *Arabidopsis thaliana* transgenic lines with overexpression of the chlorophyllide-a-oxygenase (CAO) gene from prochlorophyte cyanobacteria slowed down the initiation or stopped the senescence progress. These changes were marked when growing plants in low light and in the dark [34, 35]. With a high probability, we can expect that a shortage of Chlb leads to accelerated senescence. Besides, the data testifying that the absence of Chlb negatively affects the change of ontogenesis periods of barley has been published [36].

Chlb impact on the development of plants is convenient to be studied on model objects, the mutants unable to synthesize this pigment. *Chlorina* mutants lacking Chlb are well-known for many species, i.e. barley, corn, peas, rice, soybeans, sweet clover, wheat, rape and *A. thaliana*. Chlb biosynthesis in photosyn-

thetic tissues of higher plants is carried out by the chlorophyllide-a-oxygenase [37, 38]. The gene encoding this enzyme is presented in the genome by a single copy. Chlorophyll a (Chla) serves as the CAO substrate. Mutants by the *CAO* gene are not able to convert Chla to Chlb [39]. By the example of the most studied barley mutants of allelic series *chlorina-f2* and *Arabidopsis ch1* mutants, it was shown that a mutation in the *CAO* gene has a pleiotropic effect and is accompanied by numerous violations of the functions at the molecular, cellular and organismal levels. This indicates the importance of the pigment in the key life processes of plants.

This review discusses the Chlb functions in chloroplasts and energy metabolism of plants, as well as the role of Chlb in the regulation of the ontogenesis phases, which does not depend on the pigment photosynthetic function. Mutants of cultivated plants with the impaired Chlb biosynthesis are described as the models to identify and study mechanisms for the increase in photosynthesis and productivity. Prospects for the use of plants with the truncated size of the light-harvesting antenna complex for the increase in yield of vegetative and seed biomass are discussed.

Localization of chlorophyll b in the photosynthetic apparatus of higher plants. In plants, chlorophylls are found only in the pigment-protein complexes, as in free form, being the strongest photosensitizers, they can cause destruction of the thylakoid membranes and chloroplast stroma through the photodynamic effect. Chlb serves as an accessory light-harvesting pigment absorbing and transferring light energy to the reaction centers of photosystems. It accounts for approximately 15-25 % of the total chlorophyll content [40, 41]. Unlike Chla, which is part of the core complexes of photosystems, Chlb is found only in the light-harvesting complexes (LHC) of photosystems (LHC I and LHC II) and in the so-called minor antenna of photosystem (PS) II [42, 43]. In LHC I, Chlb accounts for about 22 % of the total amount of chlorophylls, in LHC II reaches about 43 %, and in the pigment-protein complex of the minor antenna is 31-46 % [44]. In transgenic plants with the increased Chlb biosynthesis, the antenna size can be greatly increased due to superstabilization of antenna proteins [34, 35, 45].

The role of chlorophyll b in plant energy metabolism. Chlb has a unique physico-chemical property to absorb light in the short-wave region (425-475 nm), in which Chla absorbs weakly. Chlb significantly increases light collection when the light levels are low, under mutual shading of plants in thick plantings. In the process of light collection, the energy of the excited by absorbing light quanta singlet states of pigment molecules, associated to antenna proteins, is transferred from carotenoids to chlorophylls, then from Chlb to Chla and in molecule chain order Chla reaches the reaction center of photosystems. The first two stages of energy transfer are highly efficient and occur in less than a picosecond [46, 47], while the energy transfer between Chla molecules within the same protein and between adjacent monomers takes several picoseconds [48, 49]. Chlb is responsible for transfer to Chla of about 50 % of the energy absorbed by carotenoids [50]. The efficiency of absorption of light energy and its transfer to the photosystems of mutants unable to synthesize Chlb is significantly reduced.

We should also mention the so-called red forms of chlorophylls, which are represented by Chla and Chlb located on the antenna proteins of PS I. The absorption and fluorescence spectra of these forms are shifted into the far red region [51], which makes them able to capture light energy in this range and transfer it to the reaction centers of PS I against the energy gradient in low light conditions. Such transfer is possible at physiological temperatures due to thermal energy, through which the energy gap between the donor and the acceptor is

overlapped. Such spectrum range extension due to the chlorophyll red forms provides absorption of almost 40 % of light energy in shading [52].

At high light output intensity, the chlorophyll molecules are involved in the process opposite to light collection — the diffusion of the absorbed light energy excess in the form of heat (non-photochemical quenching) potentially dangerous for plants. The functions of individual Chlb molecules are different in photoprotection. Thus, the efficient quenching of the excited chlorophyll singlet states is carried out by clusters of the paired Chla-Chlb dimer and zeaxanthin [53]. These quenching centers are localized on the minor antenna proteins of PS II [53]. For quenching of triplet chlorophyll states, in the vicinity of the neoxanthin binding site on the antenna proteins Chlb has a maximum value: in its absence, the production of singlet oxygen increases sharply [54]. It should be noted that mutants lacking Chlb, as a rule, have a strong oxidative stress, primarily, due to high production of singlet oxygen [55-56]. Since the main source of singlet oxygen in chloroplasts is PS II, these mutants may have obstruction of outflow of electrons from the reaction center of PS II into the electron transport chain (ETC). Recently, experimental evidence for this hypothesis has been obtained [57].

Chlorophyll b as a regulator of the antenna size. According to modern concepts, Chlb functions in photosynthesis are not limited to light collection and light scattering. It is known that the ratio of Chla:Chlb in high light is higher than in low one. The regulation of Chlb synthesis is essential for adaptation of plants to light of varying intensity [58]. Chlb is a major regulator of the antenna size of the photosynthetic apparatus: Chlb binding with the antenna proteins of LHC stabilizes it, and the initial reaction of Chlb catabolism activates a cascade of proteins that carry out disassembly of the antenna. Because Chlb is concentrated only in the antenna, the reduced antenna protein content leads to the change of the Chla:Chlb ratio. The stabilization mechanism of the antenna proteins with Chlb participation was described for LHCB1 [59]. In Chlb, 7-formyl group pulls electron density of magnesium central atom to the periphery of the molecule; therefore, the positive charge of magnesium is shielded by the electron cloud less than in the Chla molecule. In this regard, Chlb is easier than Chla forms electrostatic bonds with Lewis bases, namely with the carbonyl groups of the peptide chain. In addition, between the protein and the 7-formyl group, the formation of hydrogen bonds is possible. Binding Chlb to the protein leads to the fact that the conformation of the latter becomes more stable and allows it to gain a foothold in the membrane [59]. It is important to note that in the case where the molecule of LHCB1 protein is not bound to Chlb, its degradation occurs and LHC II cannot develop. It is known that in Chlb absence in chloroplasts, the contents of some other antenna proteins are reduced; there may be a similar mechanism, although experimental evidence has not yet been received. However, it can be assumed that the work of the CAO enzyme is coordinated with the import systems of synthesized in the cytosol apoproteins of the antenna complexes in chloroplasts.

Recent studies have allowed establishing that Chlb has an impact not only on the assembly of antennas, but also on the degradation of antenna proteins [60, 61]. The synthesis of apoproteins of LHC II decreases at the beginning of senescence, but due to the relatively high stability these proteins are detected in the leaves, even at its later stages [62]. While the chlorophylls are bound to proteins, the latter are not accessible to proteases [18, 62-64]. Chlb catabolism is impossible without its turning into Chla [61]. The reaction is catalyzed by two enzyme isoforms of chlorophyll-b-reductase: non-yellow coloring 1 (NYC1) and NYC1-like [65]. From this stage, the disassembly of LHC II starts [18]. NYC1

does not accumulate in Chlb absence; this protein is undetectable in *Arabidopsis* mutants lacking Chlb [66]. On the whole, Chlb synthesis and catabolism are regulated by the principles of negative and positive feedback respectively: in Chlb excess, the CAO enzyme is subjected to degradation [42], which allows the cell to maintain a low pigment content, and for the accumulation of NYC1 protein, Chlb, on the contrary, is necessary [66]. This data confirms the role of Chlb as the main regulator of the size and light-harvesting capacity of the photosynthetic antenna [44].

Participation of chlorophyll b in the maintenance of the supramolecular organization of thylakoid membranes. In chloroplasts of the mutants with impaired Chlb biosynthesis, an ability to form grains is reduced [67, 70], and also the nature of packing the pigment-protein complexes in the granule membrane is changed. The ability to form grains is reduced, because in the granule membranes, the content of integral proteins of LHC II, which play a major role in the stacking, decreases [70]. Besides, in connection with the reduced antenna protein content in grains of such plants, the pigment-protein complexes form supercomplexes with the changed composition and size [67-70]. A smaller particle size promotes a more dense packing in the granule membrane. However, this limits the lateral diffusion of membrane components, i.e. the photosynthetic proteins and the low molecular weight hydrophobic molecules, including the carrier of electrons in the photosynthetic electron transport chain of plastoquinone [71]. Recent studies have revealed that diffusion limitations hamper the timely repair of the damaged photosynthetic complexes, which prevents normal work of the latter [71]. Thus, part of the pleiotropic effects caused by *CAO* mutation in *chlorine* plants with a high probability is due to the lateral mobility limitations of membrane components of thylakoid membranes in connection with the changed stoichiometry of photosynthetic complexes because of Chlb lack. This assumption is supported by recent studies of *chlorina* mutants lacking Chlb, in barley and *A. thaliana* [57].

Participation of chlorophyll b in the regulation of the ontogenesis. Chloroplasts are the most important sources of signaling for other organelles and the cell in general. The retrograde signaling pathway from chloroplasts and mitochondria to the nucleus modulates the anterograde control in accordance with the needs of the cell [72-74]. In the absence of signaling from chloroplasts, the expression of several nuclear genes encoding proteins of these organelles, including the antenna proteins of LHC, is inhibited [74]. For chloroplasts, signaling is associated primarily with the photosynthetic function, and since the photosynthesis intensity is influenced by various factors, signaling from chloroplasts can serve as sensors of environmental conditions [75]. Among the major sources of retrograde regulation signaling there are the formation of tetrapyrroles, the expression of chloroplast genes, the change in the redox state of ETC components and the formation of reactive oxygen intermediates (ROI) [76, 77]. In addition, an important source of plastid signaling is the stability of pigment-protein complexes. This signaling carries information on environmental conditions and the age of the cell [35, 38, 65, 77].

Stay-green mutants preserving steady green coloring at later ontogenesis stages, when senescence begins in the wild type, which is accompanied by yellowing of leaves, can serve as an example of plants with a very high degree of stabilization containing chlorophyll of pigment-protein complexes. *Stay-green* mutants are known in many plant species. In particular, they include Mendelian pea mutants with green color of the seeds. There are functional and cosmetic phenotypes in *stay-green* mutants. In the functional one, the expression of senescence-associated genes (SAG) decreases and the intense photosynthesis remains

longer than in wild-type plants. In the cosmetic phenotype, senescence of mutants is induced in the same way as in wild-type plants. Moreover, they have the reduced intensity of photosynthesis, but the coloring remains green. Such phenotype is observed in mutants by *SGR* (*Stay-GReen*) genes encoding components of a complex involved in the degradation of proteins and chlorophylls of LHC II, including Chlb [34, 78]. The components of this complex are the chlorophyll catabolism enzymes (CCE), including NYC1 [62], and the very LHC II [34]. At the knockout of genes encoding proteins of CCE, stay-green phenotype is also observed [35, 65].

In the study of regulation of ontogenesis, mutants with the functional stay-green phenotype, for example, autophagy gene mutants, are of particular interest. As it is known, autophagy plays an important role in recycling of chloroplast proteins, primarily ribulose bisphosphate carboxylase/oxygenase (rubisco), especially during senescence [79]. Unable to autophagy *atg*5 mutants under mild abiotic stress, when in the wild type early senescence was induced and *SAG* genes activated, demonstrated the functional stay-green phenotype, i.e. the delayed onset of senescence [80]. It still remains unclear why in some cases the functional stay-green phenotype is implemented, and in others, when the LHC II degradation complex formation is affected directly, the "cosmetic" one is involved.

Even more intriguing is the fact that the functional stay-green phenotype appears in plants due to the accumulation of Chlb above normal. In transgenic *Arabidopsis* plants, the overexpression of the *CAO* gene from prochlorophyte cyanobacterium led to overproduction of Chlb, since, in contrast to the endogenous enzyme in plants, this enzyme in plant cell is not exposed to the regulation by the feedback principle. The Chlb content in such plants was so great that it replaced Chla in the core antenna of PS I and PS II, and the size of the light-harvesting antenna and its stability were very high [34, 35]. These transformants showed the functional stay-green phenotype and differed from wild-type plants in the delayed onset of leaves senescence both at a shortage of light and in the dark [34, 35]. Perhaps, superstabilization by Chlb of pigment-protein complexes in the light-harvesting systems and prolongation of their active functioning change the number of still unidentified signaling molecules necessary for switching the ontogenesis programs, which leads to the modulation of genome expression, including the reduced expression of *SAG* genes. The role of such signaling molecules could be performed by chlorophyll catabolites, apoproteins of LHC II lacking Chlb or products of their proteolysis. We can also assume that the long-term maintenance of the antenna of LHC II in the functional condition enhances photoprotection and, therefore, provides the reduced ROI level by the beginning of cell senescence. Probably, this slows down the initiation of subsequent stages of the senescence process. In the cosmetic stay-green mutants, the pigment-protein complex of LHC II remains, but loses the ability to interact with PS II. Thus, it is quite possible that the reason why plants obtained a negative feedback regulation of CAO enzyme was the influence of excessive amounts of Chlb on ontogenetic signaling mediated by superstabilization of the antenna of LHC II.

In the works done by us on *chlorina* mutants with a complete block of Chlb bio-synthesis (*ch1 A. thaliana* and *chlorina f2*^{3613} *Hordeum vulgare* mutants), the preliminary data on the influence of the antenna, destabilized by Chlb absence, on the time of the beginning of flowering has been obtained [36, 81]. *Chlorina* mutants of both species differed from plants of the parental lines in the later onset of floral transformation. Additionally, in 30-40 % of the barley mutants, the growth and differentiation of the ear structural elements stopped [36, 81]. In the initiation of flowering, in *chlorina* mutants the expression of *FT* gene (florigen), the main regulator of floral transformation, was disrupted, and also

the expression of genes-markers of senescence and catabolism of *SAG* and *NYC1* chlorophyll increased [81]. Violations of these processes are likely associated with changes in the retrograde signaling cascades activated by the antenna complexes of chloroplasts.

Prospects for the use of plants with the truncated light-harvesting antenna size to improve photosynthesis and productivity. In recent studies, in transgenic tobacco plants through directed modification of the light-harvesting antenna relaxation of the absorbed excessive light energy dissipating in the form of heat has been accelerated [82]. Production of vegetative biomass in such plants was higher by 15% than in the wild type. Based on these results in another study [83], the authors purposefully have examined the transgenic lines of tobacco with the truncated light-harvesting antenna size (TLA-plants) and have found a significant increase in photosynthetic productivity and growth of vegetative biomass, especially in thick plantings, noting the prospects of using TLA-plants in applications. However, manipulation through transgenesis is undesirable for crops. At the same time, *chlorina* mutants have features that bring them closer to TLA-plants, including their reduced size of the photosynthetic antenna. The data on the high intensity of photosynthesis and productivity of some chlorina wheat [84-85], soybean [86] and barley [87] mutants has been published [87], although in most cases, such mutants are characterized by the reduced photosynthesis and the growth retardation. Therefore, chlorina mutants could be promising replacement for TLA-plants, but the diversity of Chlb physiological functions described above suggests that the negative effects of *chlorina* mutations most often will level out the possible increase in photosynthesis. Such effects include the negative impact of shortage or complete absence of Chlb on ontogenetic regulation.

The nature of signaling molecules and signal transmission pathways from (de)stabilization of the antenna beyond the limits of chloroplast, which are involved in the initiation and passage of ontogenesis phases, remains unclear. However, recently we have proposed a mechanism, by which the absence of Chlb can affect the regulation of flowering [88]. In chlorina barley and arabidopsis mutants, violation of redox balance of chloroplasts changes the number and permeability of plasmodesmata, changing the conductivity of the symplastic channel that carries the macromolecule signals inducing flowering, which could be the reason for a delay of floral transformation [88-90]. This is the first work discussing the nature of the relationship between the stability of the light-harvesting antenna of the photosynthetic apparatus and regulation of flowering in plants.

Summarizing the data on Chlb functions, we can conclude that in *chlorina* mutants suppression of the photosynthetic function and productivity decrease (and, potentially, violation of the ontogenetic regulation) are due to changes in the redox balance in chloroplasts and increased production of ROI in the leaves [44, 57, 89]. Therefore, it is necessary to search for mechanisms improving the redox status of such plants. If to consider that Chlb is primarily needed at a shortage of light and for rapid rearrangements of the photosynthetic complexes caused by light flecks under the forest canopy, for agricultural crops, when grown in open spaces, many other effects of reducing chlorophyll b contents will be negligible. Furthermore, the reduction of the costs for synthesis of unnecessary for photosynthesis antenna proteins, which constitute a considerable portion of proteins in chloroplasts, will allow plants to save some resources, and the reduced light absorption by the leaves will increase the amount supplied to the leaves of lower layers in thick plantings. Our studies have shown the possibility of formation of highly productive phenotype of *chlorina f2 3613* barley mutant, when grown in open ground [36].

So, the recently discovered Chlb function associated with the regulation of the ontogenesis phases in plants deserves a detailed study. A convenient model may be mutants of *CAO* gene for Chlb biosynthesis, i.e. *chlorina-f2* (barley), *ch1* (*Arabidopsis*), as well as mutants of the *NYC* genes encoding isoforms of enzymes of Chlb catabolism. The results of such studies will be used in breeding, and also in the improvement of agrotechnical methods to ensure timely flowering and prevent early plant senescence. In general, the study of mutants with the changed Chlb biosynthesis is of practical interest to identify new mechanisms for increasing photosynthesis and crop yield.

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