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Photoprotection of Cotton in the Field

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Abstract

This chapter focuses on the mechanisms by which cotton leaves regulate and use incident light and dissipate the excess light energy when cotton suffers from drought in the field. The photoprotection of non-foliar organs, including bract, capsule wall and stem, will also be considered. This chapter includes a general description of photoprotection from the perspective of leaf movement, drought and non-foliar organs. Leaf diaheliotropic movement and wilting movement can regulate the excess light energy of the photosynthetic apparatus. Besides non-photochemical (heat) energy dissipation, the alternative electron sinks for the electron transport chains are of vital importance for resistance of the photosynthetic apparatus against excess light energy under drought. Thus, the functioning of both photosystem II (PSII) and the photosynthetic electron transport systems of cotton leaves shows a relatively high stability. Compared with leaf, bract mainly relies on high activities of thermal energy dissipation for photoprotection. Nevertheless, capsule wall of bolls is less able to dissipate energy via heat.

Keywords: cotton, leaf movement, thermal dissipation, photochemistry, ROS scavenging

1. Introduction

Sunlight is essential for photosynthesis and supports most life on earth. However, too much sunlight damages the photosynthetic machinery. The amount of light energy encountered by plants in excess of that needed for photosynthetic assimilation is termed excess light energy. When the excess light energy cannot be dissipated safely, the electron transport chain becomes

highly reduced, and electron transfer to O₂ increases, producing reactive oxygen species (ROS). ROS is very damaging to the photosynthetic apparatus, primarily photosystem II (PSII), causing photoinhibition [1–3]. To counteract photoinhibition, plants have evolved multiple photoprotective mechanisms to cope with the potentially damaging effects of excess light energy. On the one hand, acclimation to adverse conditions can occur in terms of morphological characteristics such as light avoidance associated with the movement of leaves [4, 5] and chloroplasts [6]. On the other hand, biochemical processes such as photorespiration [7, 8], the Mehler-peroxidase reaction [9], cyclic electron transport [10, 11] and thermal dissipation [12, 13] can help to dissipate excess light energy from the photosynthetic apparatus.

High-light stress is exacerbated by drought. Drought is considered to be the most limiting environment factor [14, 15]. During drought, the process of photosynthetic carbon assimilation is primarily suppressed [15, 16]. As a result, the plant has to dissipate more excess light energy in order to avoid photo-oxidative stress, thereby maintaining photosynthetic productivity under drought.

Cotton (*Gossypium* spp.) is a plant of tropical origin, an oilseed and fibre crop that is cultivated in more than 70 countries worldwide. There are four species of cultivated cotton, *G. hirsutum*, *G. barbadense*, *G. arboretum* and *G. herbaceum*, providing the world's most important textile fibre. *G. hirsutum*, commonly referred to as upland cotton, is the most extensively developed species and accounts for about 90% of total world production. *G. barbadense*, referred to as pima cotton, is valued for superior fibre properties. Thus, two cotton species, upland cotton and pima cotton, will be discussed here. In this chapter, we not only focus on the photoprotection of the leaf but also on the photoprotection of non-foliar organs, because photosynthetic production of non-foliar organs significantly contributes to the yield in cotton [17]. In addition, we emphasize results from the field experiments on cotton, not from the lab or greenhouse.

2. Leaf movement and photoprotection

Generally, leaf movement includes three types: leaf diaheliotropic movement, leaf paraheliotropic movement and leaf wilting movement. The first one provides maximum interception of sunlight, whereas both the second and the third give minimum interception of sunlight. Many researchers have reported that leaf paraheliotropic movement is a vital important way to reduce the excess light energy of the leaves generally in leguminous species [18, 19]. However, cotton has leaf diaheliotropic movement and wilting movement depending on the water status of leaves. Actually, leaf wilting movement is quite general in higher plants.

Upland cotton has leaf diaheliotropic movement, but pima cotton has no or only weak diaheliotropic movement [20, 21]. Given their maximum interception of light, the leaves of upland cotton must be accompanied by strong photosynthetic assimilation or dissipation of excess light energy. When leaves of upland cotton are restrained to the horizontal position, carbon assimilation decreases compared to diaheliotropic leaves because of less interception of light [22]. However, there is no difference in the recovery of maximal quantum yield of PSII photochemistry (F_v/F_m) between diaheliotropic and restrained leaves [22]. This means that the

leaves of upland cotton have photoprotection mechanisms to trade-off the maximum interception of light and excess light energy. A number of reports have suggested that thermal energy dissipation in the photosynthetic apparatus is involved in photoprotection in upland cotton and pima cotton [22–24]. As mentioned above, leaf diaheliotropic movement is absent or weakly expressed in pima cotton. Pima cotton has lower actual photosynthetic assimilation than upland cotton in the field even if diaheliotropic leaf movement of upland cotton resulting in high incident leaf sunlight is taken into account. However, both cotton species exhibit similar photosynthetic potential [24].

Zhang et al. [25] found that upland cotton preferentially dissipates light energy via electron transport, whereas pima cotton mainly does so through thermal energy dissipation. Indeed, Wise et al. [26] reported that electron transport limits the photosynthesis of field-grown pima cotton. Thus, using different photoprotective mechanisms, both cotton species have a strong capacity for photoprotection to maintain the activity of the two photosystems. Further, some photoprotective mechanisms, such as thermal energy dissipation and photorespiration, mitigate against excess light energy. Interestingly, in young leaves of upland cotton, the photoprotective mechanisms also operated well even when the photosynthetic apparatus was not yet fully assembled [27]. In addition, in an experiment conducted to compare cotton and soybean which differ in leaf movement under drought, cotton and soybean showed different strategies for conferring photoprotection [28].

Leaf wilting movement occurs generally under drought when the water potential of leaves and the osmotic potential of petiole cells exceed the threshold. This leaf movement may have multiple physiological significance for plants because it may reduce both water loss from the leaf and the amount of light incident on the leaf surface, the latter lowering the energy load on a leaf [29]. Leaf wilting movement becomes apparent only after several anatomical and physiological adjustments have occurred as drought develops [30]. In cotton, when leaves are not restrained to the horizontal position, the wilting movement of leaves protects water-stressed cotton plants against photoinhibition and maintains considerable carbon assimilation in the long term [5]. Clearly, passive wilting leaf movement can be a strategy for photoprotection that enables plants to survive under drought.

3. Photoprotection under drought

3.1. Drought and photoinhibition

Drought decreases CO₂ assimilation rate [31], and photosynthesis saturates at a lower PPFD in drought plants. For instance, maximum CO₂ assimilation rates under well-watered conditions are about 42.4 (upland cotton) and 37.1 (pima cotton) $\mu\text{mol m}^{-2} \text{s}^{-1}$, and 25.1 (upland cotton) and 23.9 (pima cotton) $\mu\text{mol m}^{-2} \text{s}^{-1}$ under drought, respectively [32]. The light saturation points are 2304 and 1996 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in well-watered and drought upland cotton plants, respectively [28]. In field conditions, drought is usually accompanied by other limiting factors, such as high temperature and irradiance. Therefore, when drought stress occurs

simultaneously with high irradiance, cotton plants may be exposed to an excess of excitation energy, potentially increasing the susceptibility of PSII to photoinhibition.

Zhang et al. [5] have reported that the diurnal time course of F_v/F_m is similar in both well-watered upland and pima cotton plants; the values of F_v/F_m are ~ 0.80 in the morning, after which the values decrease to ~ 0.72 at noon and recover to ~ 0.80 in late afternoon. Some reports have demonstrated that drought-stressed upland cotton plants are characterized by a higher F_v/F_m [33–35]. For example, Yi et al. [32] have reported that the pre-dawn F_v/F_m is ~ 0.85 in both upland and pima cotton under well-watered and water-deficit conditions. Sustained photoinhibition of PSII seems not to occur in field-grown cotton plants under drought since no significant decrease in pre-dawn F_v/F_m has been reported. This phenomenon has been observed earlier by Genty et al. [36] who demonstrated that water stress does not induce sensitization to photoinhibition in cotton. Additionally, Yi et al. [37] found that the activities of photosystem II (PSII) and photosystem I (PSI) show almost no changes during water deficit and recovery, though water deficit leads to a reversible reduction in the photosynthetic rate. Therefore, the photosystems of field-grown cotton plants are relatively stable under drought stress.

As describe above, drought stress decreases CO_2 assimilation rate but does not induce sustained photoinhibition of PSII in field-grown cotton plants. Therefore, field-grown cotton plants may possess multiple photoprotective strategies to cope with drought stress (see below).

3.2. Thermal dissipation of absorbed light energy

Plants can dissipate excessive light energy harmlessly as heat [38–40] which is called ‘thermal energy dissipation’. Thermal dissipation, measured as non-photochemical quenching of Chl fluorescence (NPQ), is related to the pH gradient across the photosynthetic (thylakoid) membrane and promoted by the activity of the xanthophyll cycle, with conversion of violaxanthin to zeaxanthin, via antheraxanthin, by the catalyst violaxanthin de-epoxidase (VDE) [41]. Demmig-Adams et al. [42] showed that in well-watered sunflower plants, more than 50% of absorbed light is thermally dissipated at midday. In well-watered cotton plants, $\sim 44\%$ of the absorbed light energy is used in photosynthetic electron transport (photosynthesis and photorespiration), and the remaining 56% is dissipated as thermal energy [43]. Kornyejev et al. [44] and Massacci et al. [33] also reported that non-photochemical energy dissipation serves as the major photoprotective mechanism when light energy absorption becomes excessive in cotton plants. Under moderate and severe drought, thermal dissipation increases up to 70–82% of the total absorbed light in cotton plants [43]. In addition, Zhang et al. [28] and Yi et al. [32] observed that pima cotton has generally higher thermal energy dissipation capacity than upland cotton under well-watered conditions. However, Genty et al. [36] and Yi et al. [32] also found that water deficit does not increase thermal dissipation in upland cotton plants. A similar result was reported by Inamullah and Isoda [45] who found that there is no significant change in photochemical reflectance index (PRI) (which is correlated with the epoxidation state of the xanthophyll cycle) in upland cotton under water deficit. Perhaps different cotton cultivars, studied under different experimental conditions such as temperature and irradiance, exhibit different thermal energy dissipation capacities in response to drought (**Figure 1**).

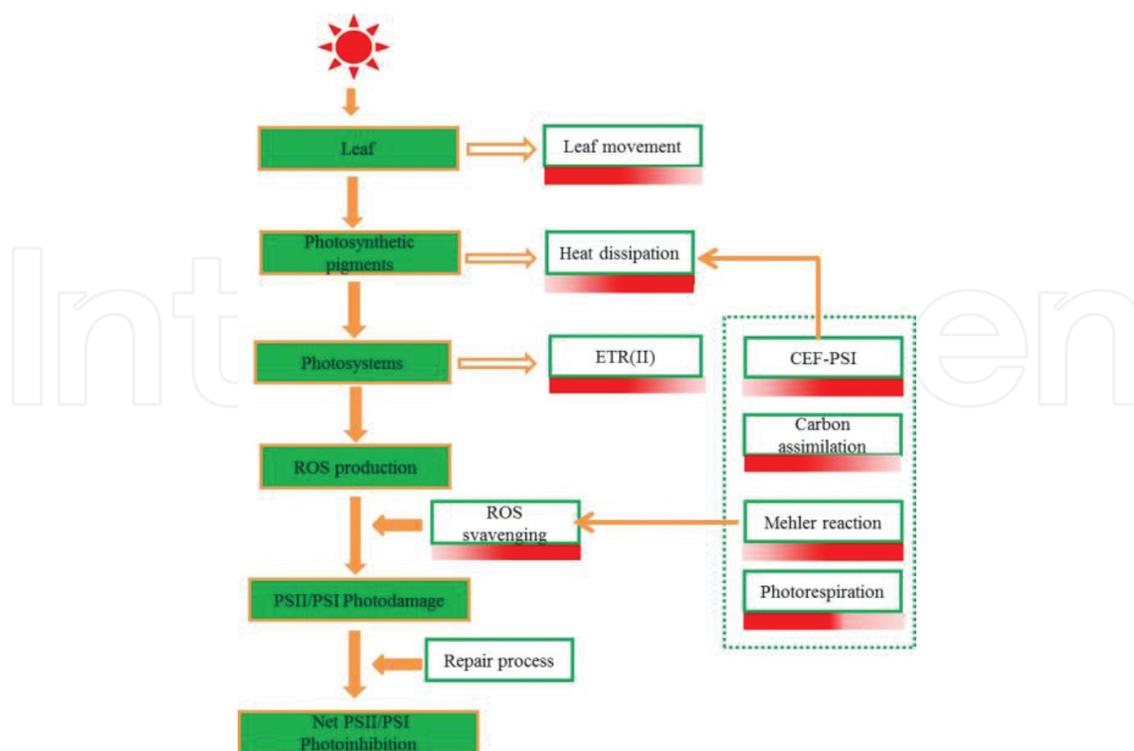


Figure 1. A model of photoprotection mechanisms in field-grown cotton plants under drought. Cotton leaves can utilize diheliotropic movement and wilting movement to adjust the absorption of light energy. In addition, leaves can dissipate excessive energy through electron transport pathways, including photorespiration, Mehler reaction and cyclic electron transport. Furthermore, ROS scavenging and repair process also have an important role in avoiding sustained photoinhibition in leaves. Arrow indicates the induction processes, and the shades of red indicate the response of biochemical processes to drought.

3.3. Photoprotection through photochemistry

It is well known that under normal conditions much of the photosynthetic electron flow is used to drive the photochemical reaction, with conversion of the absorbed light energy to active chemical energy stored in ATP, NADPH and Fd_{red} . The excitation energy, distributed in favour of photochemical reactions, is mainly used for photosynthetic carbon reduction, photorespiratory carbon oxidation and alternative electron transport. A few studies have reported that when the CO_2 assimilation rate is decreased under drought, cotton plants can dissipate excessive energy through other electron transport pathways, including photorespiration [23, 32–34], Mehler reaction [23, 32] and cyclic electron transport [46, 47].

3.3.1. Photorespiration

Photorespiration is the reaction of O_2 with ribulose-1,5-bisphosphate (RuBP) catalysed by ribulose-1,5-bisphosphate carboxylase/oxygenase (rubisco), producing glycolate-2-P [48]. Photorespiration is second only to photosynthesis as the most important mechanism for utilization of electrons, occurring at high rates in the leaves of C_3 plants [8]. Under well-watered and saturating light conditions, photosynthesis and photorespiration dissipate 20–30%

and 10–20% of absorbed light, respectively [49]. Similarly, Björkman and Schäfer [43] reported that in well-watered cotton plants, 25% of the absorbed light is used for photosynthesis and 19% for photorespiration. Tourneux and Peltier [50] demonstrated that photorespiration is a substantial sink for electrons in leaves at high and low relative water content (RWC). Chastain et al. [34] and Yi et al. [23] concluded that water deficit increases photorespiration since photosynthesis is decreased by stomatal (CO_2) limitation in field-grown cotton plants. However, Cornic and Fresneau [51] pointed that during mild drought, photosynthesis and photorespiration are the main electron sinks for PSII activity. Further, Massacci et al. [33] demonstrated that cotton leaves can increase the capacity for photorespiration to prevent photodamage during the onset of drought stress. A similar result was reported by Yi et al. [32] who showed that under mild water deficit, pima cotton appears to rely on enhanced photorespiration to dissipate light energy while under moderate water deficit, the contribution of photorespiration decreases. Actually, all the results that reported increased photorespiration under conditions of CO_2 limitation have been based on relative values (such as the ratio of photorespiration to photosynthesis or the ratio of oxygenation to carboxylation) or indirect data [23, 32, 33, 43, 52, 53]; the absolute rate of photorespiration decreases [28, 52, 54, 55].

3.3.2. Mehler-peroxidase reaction or the water-water cycle

The Mehler-peroxidase reaction (MPR) is the reduction of O_2 to water in PSI by the electrons generated in PSII from water [56]. The functions of the Mehler-peroxidase reaction for protection from photoinhibition are to scavenge reactive oxygen species (ROS), thereby protecting chloroplasts from the direct effects of ROS [9]. Badawi et al. [57] reported that over-expression of ascorbate peroxidase (APX) in tobacco chloroplasts show enhanced tolerance to salt and drought stresses. In addition, the Mehler-peroxidase reaction can regulate CO_2 fixation and excess energy dissipation through adjustment of the production ratio of ATP/NADPH. Ziem-Hanck and Heber [58] demonstrated that under anaerobic conditions, no CO_2 is fixed in intact chloroplasts because of a low ratio of ATP/NADPH, but the addition of O_2 allows CO_2 assimilation to start by increasing the production of ATP through the Mehler-peroxidase reaction. Osmond [7] indicated that higher ATP/NADPH is required to operate photorespiration, and that the Mehler-peroxidase reaction may supply additional ATP for photorespiration. Neubauer and Yamamoto [59] reported that the Mehler-peroxidase reaction contributes to the generation of a transmembrane proton gradient for thermal dissipation of excess absorbed light energy. Furthermore, the Mehler-peroxidase reaction itself can dissipate excess electrons using O_2 as the electron acceptor.

Wingler et al. [60] suggested that at low water potential, the increased electron flow to O_2 was mainly due to the Mehler reaction. Biehler and Fock [55] observed that 29% of the photosynthetic electrons are consumed in the Mehler-peroxidase reaction in drought-stressed wheat leaves. Our recent results showed that water deficit increases the electron flux for O_2 -dependent alternative electron transport in upland cotton plants, which is related to the Mehler-peroxidase reaction activity [23]. However, studies conducted with different species under drought stress provide partly contradictory results on the role of Mehler-peroxidase reaction. Yi et al.

[32] found that the contribution of the Mehler-peroxidase reaction to excess electrons dissipation is very low in water-deficit pima cotton. Similar results were also reported by Haupt-Herting and Fock [61] in tomato and Flexas et al. [53] in grapevines. In addition, Björkman and Schäfer [43] reported that energy dissipation through photorespiration plus the Mehler-peroxidase reaction gradually decreases with increasing water deficit in cotton plants, and the contribution of the Mehler-peroxidase reaction to total dissipation is low or null.

3.3.3. Cyclic electron transport

Cyclic electron flow (CEF) around PSI (CEF-PSI) is the recycling of electrons from PSI to the plastoquinone pool and the cytochrome b6f complex via reduced Fd or NADPH [10, 62–65]. It is well known that CEF-PSI is essential for protecting PSII against excess excitation pressure because CEF-dependent build-up of a ΔpH across the thylakoid membrane helps the activation of NPQ [10, 66–70] and prevents the inhibition of the repair of photodamaged PSII [3, 11]. The result can be explained by the fact that NPQ suppresses the production of ROS [71].

A number of studies indicated that CEF-PSI plays a significant physiological role in plant responses to drought or desiccation [11, 68, 70, 72, 73]. Singh et al. [46] demonstrated that CEF-PSI plays an important role in tolerance under drought stress in upland cotton plants, which are grown in a growth chamber. A similar result was also observed in our recent experiment on greenhouse-grown upland cotton, using the method of Kou et al. [70] to estimate CEF-PSI (data not shown). In addition, Singh et al. [47] compared the activity of CEF-PSI in drought stress upland and pima cotton plants and concluded that drought increases the activity of CEF-PSI in both cotton species, but that pima cotton showed lower CEF-PSI under drought as well as well-watered condition in comparison to upland cotton. However, our recent studies with field-grown cotton under water-deficit conditions showed that pima cotton possessed a higher CEF-PSI capacity compared with upland cotton (data not shown). Different grown conditions and methods may result in different conclusions, and so far, there is still a considerable lack of knowledge about the photoprotective functions of CEF-PSI in field-grown cotton. Therefore, CEF-PSI in cotton requires further study.

3.4. Scavenging of reactive oxygen species

Drought may induce an oxidative stress due to the inhibition of photosynthesis, resulting in the production and accumulation of reactive oxygen species (ROS) at the photosystems [9]. ROS can damage the photosynthetic apparatus, through oxidation of lipids, proteins, carbohydrates and nucleic acids [74, 75]. The major antioxidative systems in the plant, including superoxide dismutases (SOD), ascorbate peroxidase (APX), peroxidase (POD) and catalase (CAT), together with carotenoids, ascorbate (AsA) and glutathione (GSH), provide cells with highly efficient machinery for detoxifying O_2 and H_2O_2 [76]. Additionally, some osmolytes such as proline and glycine betaine can also contribute to the relief of oxidative stress [77].

Mahan and Wanjura [78] reported that the content of AsA and the activity of APX are increased in response to water stress, but the GSH amount and form are not. Further, there is no

significant change in the levels of malondialdehyde (MDA), an indicator of cell-membrane damage. Therefore, they concluded that antioxidative metabolism in field-grown cotton plants exposed to drought stress is sufficient to protect against oxidative damage. A similar result was also observed in our experiment [37]. Over-expression of APX improves the antioxidative system and enhances tolerance of cotton plants against low temperature [79]. In addition, our results also showed that the activities of SOD and POD are increased under water deficit [23, 37] and that the activities of SOD and APX increase under water deficit in upland cotton, while those enzymes do not respond to water deficit in pima cotton [32]. However, Kawakami et al. [80] also reported that the activity of SOD in water-stressed cotton plants is significantly decreased compared to the well-watered plants. It appears that the levels of the antioxidative systems may increase, decrease or remain unchanged depending on plant species, the period and the intensity of water deficit and plant age or developmental stage [81]. Additionally, De Ronde et al. [82] and Yi et al. [37] reported that with increasing water deficit there is a progressive increase in free proline in cotton plants.

3.5. Repair of photodamage

Although there are multiple photoprotective mechanisms, photo-oxidative damage to the photosynthetic apparatus is an inevitable process under drought. Takahashi and Badger [3] reported that net photoinhibition only occurs when the rate of damage exceeds the rate of repair. Chow and Aro [83] reported that during the course of a sunny day, the entire population of PSII could be photoinactivated if repair is inhibited. Aro et al. [84] suggested that fast recovery of damaged PSII helps the plant reduce the susceptibility to photoinhibition. Lee et al. [85] and Kato et al. [86] indicated that a higher rate of turnover of D1 protein plays a crucial role in photoprotection in high light-grown plants. A similar result was also observed by Oguchi et al. [87] in spinach and *Alocasia* leaves. Field-grown cotton plants are often exposed to high irradiance, but there is no sustained net photoinhibition of PSII. It means that the rate of repair must match the rate of damage to avoid the occurrence of net photoinhibition in field-grown cotton plants under water deficit. Indeed, the rate coefficient of repair of upland cotton increases steadily with irradiance up to at least 1300 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$, provided there is no oxidative stress [88].

3.6. Non-foliar organs and photoprotection

Aschan and Pfanz [89] in a review have concluded that photosynthesis of non-foliar organs is an important, additional contribution to carbon acquisition and yield. Examples are the panicles of rice, the ear of wheat [90, 91], the spikes of barley and the fruit in tomato [92]. Besides leaves, many parts of cotton, including stem, bract and boll, contain chlorophyll and, therefore, capture light energy to perform photosynthesis. The stems, bracts and the capsule wall of bolls contribute to carbon gain [93–96]. In cotton, Hu et al. [17] have reported that darkening the non-foliar organs reduced the boll weight by 24.1 (boll) and 9% (main stem) and the seed weight by 35.9 (boll) and 16.3% (main stem). Therefore, we have concluded that non-foliar organs of cotton are of vital importance to the yield at the late growth stage due to leaves tending to senesce earlier than non-foliar organs [17].

Undoubtedly, the leaves are more physiologically active, with greater rates of photosynthesis and respiration than the bracts and capsule walls [17, 93, 95]. As we can see in the field, however, non-foliar organs and leaves are normally exposed to similar irradiance. Therefore, one wonders whether the non-foliar organs have different ways of dissipating the excess light energy safely to confer on photoprotection. Zhang et al. [97] have conducted an experiment to compare the characteristics of PSII behaviour in leaves and non-foliar organs and concluded that lower PSII photochemical activity in non-foliar organs may result from limitations at the donor side of PSII and the acceptor sides of both photosystems. Compared to leaves, the thermal dissipation fraction of light absorbed by the PSII antennae is the highest in the bract and the lowest in the capsule wall of bolls. Furthermore, the capsule wall of bolls is characterized by a smaller combined constitutive thermal dissipation (with little dependence on irradiance) and dissipation as fluorescence emission [97]. Furthermore, Hu et al. [98] suggested that the bract dissipates its absorbed light energy via Δ pH- and xanthophyll-regulated thermal dissipation for photoprotection, aided by the high activities of antioxidative enzymes. The main stem preferentially uses both light-regulated and light-independent non-photochemical quenching to confer photoprotection. The capsule wall of bolls is less able to dissipate energy via heat. Thus, its main photoprotective mechanisms of the capsule wall of bolls seem to be direct quenching of the energy by abundant carotenoids and light-independent constitutive thermal dissipation. Furthermore, because of lower activities of antioxidative enzymes, the capsule wall of bolls is less able to scavenge reactive oxygen species.

In addition, we have proposed that the photosynthesis from non-foliar organs is important for increasing cotton yield especially under drought conditions [98, 99]. Non-foliar organs (bract and capsule wall) show less ontogenetic decrease in photosynthetic capacity, photosynthetic enzyme activity and better antioxidative systems than leaves in response to drought stress. Thus, the relative photosynthetic contribution of the non-foliar organs to the whole plant is expected to increase under drought [98]. In the bract, both photorespiration and energy dissipation appear to alleviate photoinhibition and play important roles in photoprotection [100].

4. Conclusion

A brief review of the photoprotection of cotton in the field has been presented. We included a general description of photoprotection from the perspective of leaf movement, drought and non-foliar organs. Clearly, leaf diheliotropic movement and wilting movement can regulate the excess light energy of the photosynthetic apparatus. Besides non-photochemical (heat) energy dissipation, the alternative electron sinks for the electron transport chains are of vital importance for resistance of the photosynthetic apparatus against excess light energy in the field. Thus, both the functioning of PSII and the photosynthetic electron transport systems of cotton leaves show a relatively high stability. Compared with leaf, bract mainly relies on high activities of thermal energy dissipation for photoprotection. Nevertheless, the capsule wall of bolls is less able to dissipate energy via heat.

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