16 External and Internal Factors Responsible for Midday Depression of Photosynthesis

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CONTENTS

I. INTRODUCTION

Midday depression of photosynthesis occurs in many plants and significantly affects crop yields. Since it was discovered at the beginning of the last century, many studies have been carried out, and several hypotheses, such as feedback inhibition of photosynthesis resulting from assimilate accumulation, stomata closure, enzyme deactivation, and reversible decline in photochemical activity, have been proposed to explain the phenomenon [1–4]. In recent years, the midday depression has been scrutinized by modern techniques. However, its causal mechanism is still not established [4]. Based on available data, the ecological, physiological, and biochemical factors related to the midday depression are analyzed and the possible mechanisms and adaptive importance are discussed in this chapter.

II. THE PHENOMENON

A. Pattern of Diurnal Variation for Photosynthesis

Under natural conditions there are two typical patterns of photosynthetic diurnal course [5]. One is one-peaked, that is, net photosynthetic rate increases gradually with the increase in sunlight intensity in the morning, reaches its maximum around noon, then decreases gradually with the decrease in sunlight intensity in the afternoon. Another is two-peaked, that is, there are two peak values of net photosynthetic rate, one in late morning and the other in late afternoon with a depression around noon, the so-called midday depression of photosynthesis, as shown in Figure 16.1 (curves 1 and 2).

B. Midday Depression of Photosynthesis

Midday depression of photosynthesis is a common phenomenon. It may occur in many species of plants including C_3, C_4, and calmodulin (CAM) plants under a particular combination of environmental conditions [6]. In plants that show midday depression, however, it does not necessarily occur in all situations. For example, in some plants midday depression occurs in summer but not in winter [7,8]. In addition, this phenomenon is remarkable only in the upper-layer leaves of cassava [9].

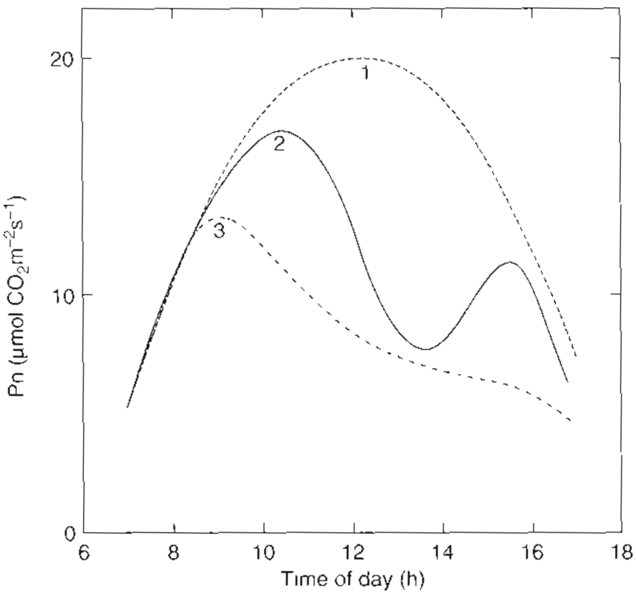

FIGURE 16.1 Schematic diagram of diurnal variation of net photosynthetic rate in plant leaves. Curve 1, one-peaked diurnal course; curve 2, two-peaked diurnal curve; curve 3, one-peaked diurnal course, but with severe midday depression.

When the midday depression is serious, no second peak in the diurnal course of photosynthesis appears [10]. The single-peaked curve of the diurnal course of photosynthesis in such cases differs very much from those where the midday depression is absent. For the former the peak value of net photosynthetic rate is often in the morning (Figure 16.1, curve 3), but the peak value is at noon for the latter (Figure 16.1, curve 1).

III. ECOLOGICAL FACTORS RESPONSIBLE FOR MIDDAY DEPRESSION

A. Sunlight

In general, the two-peaked diurnal course of photosynthesis occurs on clear days with intense sunlight, while the one-peaked diurnal course occurs on cloudy days with weak sunlight [2,11]. Naturally, it is assumed that the midday depression is caused by intense light. Nevertheless, it may occur at medium light of about 500 μmol photons/m^2/sec [12,13]. Although intense light is not a necessary condition for midday depression to occur, in fact, intense sunlight is the most important ecological factor for midday depression. In some cases, it may lead indirectly to midday depression through low humidity and high temperature because intense sunlight is the primary driving force of diurnal variation in many environmental conditions. In other cases, it may result in midday depression through downregulation of photosynthetic capacity caused by intense sunlight, as observed in some woody plants [14].

B. Air Temperature

Herppich et al. [15] reported that *Protea acaulos*, a prostrate fynbos shrub, often experiences very low air humidity at leaf temperatures over 10°C higher than mean air temperature, and shows a pronounced midday depression of gas exchange at the end of the dry summer season, independent of water supply. However, artificially lowered leaf temperatures in a gas exchange cuvette can prevent this midday depression almost completely under the same light conditions. Therefore, they considered that leaf temperature, directly or via the vapor pressure deficit (VPD) between leaf and air, rather than plant water status, is the determinant of midday depression. Around noon, high temperature can enhance CO_2 efflux from respiration or photorespiration, causing a decline in net

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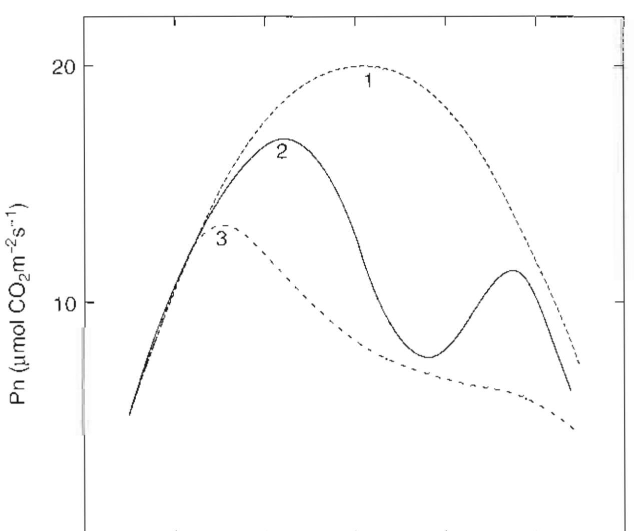

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C. Air Humidity

Photosynthesis in many plants is highly sensitive to changes in air humidity, or, more precisely, VPD. One-peaked diurnal course of photosynthesis could be artificially induced by high air humidity even at the end of the dry season when two-peaked patterns are common in natural weather [17]. Under low air humidity the two-peaked diurnal course of photosynthesis was observed in apricot even when soil water status was good [18]. Net photosynthetic rate in cassava decreased rapidly as VPD increased [19]. In wheat a significant negative correlation between net photosynthetic rate and air saturation deficit was observed. Furthermore, increasing air humidity led to an increase in net photosynthetic rate and to disappearance of midday depression [20]. It was found in maize that both high photon flux density and high air saturation deficit were necessary for afternoon inhibition of photosynthesis to appear [21]. The afternoon declines in canopy CO_2-exchange rates found in a number of species were associated with an increase in VPD [22]. It was observed that enhanced air humidity increased not only net photosynthetic rate but also the optimal temperatnre of photosynthesis in wheat leaves [23]. The nonstomatal mechanism by which air humidity affects photosynthesis is not clear [24].

Due to its effect on VPD, influence of temperature is often closely linked to air humidity impact on the diurnal course. Raschke and Resemann [13] demonstrated the dominant role of humidity in the induction of midday depression in *Arbutus unedo* leaves. The depression occurred at a constant leaf temperature in their experiment when a threshold in VPD was exceeded, but the depressions were hardly noticeable when VPD was held constant and leaf temperature was allowed to vary within a certain range.

Low air humidity has been considered an important ecological factor responsible for the midday depression [13,25–30].

D. Soil Water Status

Among environmental factors, soil water status seems to be a decisive factor in midday depression of photosynthesis. For instance, with a decline in soil water potential, a one-peaked diurnal course of photosynthesis in soybean leaves became two-peaked, and midday depression became more severe [31]. After heavy rain, midday depression disappeared almost completely in wheat leaves on the following day [32]. Leaf water potential at dawn is a reflection of soil water status. As the leaf water potential at dawn declined, the pattern of the diurnal course of photosynthesis in soybean leaves changed from one-peaked to two-peaked, and the midday depression gradually became severe [33]. In addition, it was observed that midday depression of photosynthesis occurred in pot-grown, but not in field-grown, wheat under the same aboveground conditions (D.-Q. Xu et al., unpublished data). This difference was also reported between field-grown and pot-grown soybean plants [34]. Of course, the effect of soil water status on leaf photosynthesis is indirect. Many studies have suggested that under drought conditions stomatal closure often plays the main role in the decline in leaf photosynthesis, that is, photosynthetic biochemistry and photochemistry are not impaired by the lack of water [35].

E. Carbon Dioxide Concentration in the Air

Midday depression of photosynthesis is often accompanied by decreased air CO_2 concentration around noon. Some researchers consider the decreased CO_2 concentration as an important ecological factor leading to midday depression [36]. However, according to Xu et al. [20], the extent of the decline in CO_2 concentration did not match the extent of the midday depression. Moreover, the air CO_2 concentration did not increase when the second peak of net photosynthetic rate in the daily course appeared, indicating that the diurnal variation pattern in net photosynthetic rate is not dependent on the air CO_2 concentration. The midday depression in *Quercus suber* persisted even at a CO_2 partial pressure of 250 Pa [37]. It appears that decreased air CO_2 concentration around noon is not an important ecological factor for midday depression.

IV. PHYSIOLOGICAL FACTORS RESPONSIBLE FOR MIDDAY DEPRESSION

A. Stomatal Closure

In some plants midday closure of stomata occurs [5,38], and it is often coincident with midday depression of photosynthesis [13,18,20]. However, whether the midday closure of stomata is the cause of midday depression of photosynthesis cannot be established only on the basis of a change in stomatal conductance. According to Farquhar and Sharkey [39], stomatal closure can be considered an important cause of decline in photosynthetic rate only when the intercellular space CO_2 partial pressure (C_i) also decreases.

A decreased C_i was observed when midday depressions in net photosynthetic rate and stomatal conductance occurred in bamboo [14,40], wheat [41], soybean [42,43], *Ginkgo biloba* [44], and strawberry [45]. These reports indicate that stomatal partial closure is indeed responsible for midday depression of photosynthesis.

Although among the 37 cases of midday depression investigated, 19 were accompanied by a reduction in C_i of 1 to 3 Pa, Raschke and Resemann [13] concluded that the midday depression of photosynthesis in leaves of *A. unedo* was not caused by stomatal closure. However, it is not clear whether nonuniform stomatal closure occurs in their experiments. Due to the patchy closure of stomata under stress conditions [46–48], overestimated C_i may lead to the misinterpretation that the reduction in photosynthesis caused by stomatal closure results from nonstomatal factors.

In general, C_i is calculated from leaf gas exchange data according to the equation $C_i = C_a - A/G_c$, where C_a and C_i are the partial pressures of CO_2 in the air and inside the leaf, and A and G_c are net photosynthetic rate and stomatal conductance to diffusion of CO_2, respectively [39]. From this equation, it is very clear that C_i decreases rarely in proportion to the decrease in A when A and G_c decrease simultaneously. In fact, during midday depression the magnitude of C_i decrease is often much less than that of the decrease in net photosynthetic rate. For instance, compared with the value of the first peak, net photosynthetic rate in wheat leaves decreased by about 48% during midday depression, while C_i decreased by only 11%, although an analysis showed that stomatal closure was the most important physiological cause of midday depression [41]. It is likely that an increased CO_2 efflux from respiration or photorespiration is responsible for the difference in the extent of decline between A and C_i because the CO_2 efflux leads to a decrease in A and an increase in C_i. Therefore, stomatal limitation of photosynthesis during midday depression cannot be precluded based only on the fact that the extent of C_i decline is less than that of the decline in net photosynthetic rate. Furthermore, when A and G_c evidently decline in a coordinated way, namely, the plot of A against G_c is linear, or patchy closure of stomata occurs, calculated C_i from the equation is unchanged because A/G_c is constant, but actually C_i is changed. Thus, such an apparently constant C_i is likely to mask the fact of stomatal limitation, forming an artifact of nonstomatal limitation of photosynthesis. In other words, only when C_i increases can one confidently say that the decline in net photosynthetic rate results from a nonstomatal factor.

B. Enhancement of Respiration and Photorespiration

There is evidence that a rise in respiration or photorespiration near noon is one of the physiological causes of midday depression. Thus, in the leaves of *Q. suber* a substantial increase in the CO_2 compensation point has been observed during midday depression of photosynthesis [37], implying that respiration and photorespiration are enhanced by the higher leaf temperature around noon. In satsuma mandarin (*Citrus unshiu* Marc) midday depression of both net photosynthetic rate and apparent photosynthetic quantum efficiency has been attributed to increased photorespiration around noon [49]. The increased photorespiration may be a response to high light or the decline in C_i due to midday closure of stomata.

C. Increase in Mesophyll Resistance

Mesophyll resistance to CO_2 diffusion should be considered when one explores further the physiological causes of midday depression. In soybean leaves both stomatal resistance and mesophyll resistance increased during the midday depression of photosynthesis [33]. Mesophyll resistance seems to play a more important role in some conifers [2].

D. Decrease in Leaf Water Potential

As a consequence of the larger evaporative demand near noon, there is usually a midday depression of leaf water potential. The diurnal course of change in leaf water potential similar to that of photosynthesis was observed in some conifers [2]. In some experiments with *Helianthus annuus*, however, no unique relationship among stomatal conductance, photosynthetic rate, and leaf water potential was observed, but stomatal conductance and net photosynthetic rate decreased when about two thirds of the extractable water in the soil had been used irrespective of the leaf water potential. Therefore, it was suggested that soil water status, not leaf water status, affected the stomatal behavior and photosynthesis of *H. annuus* [50].

E. Development Stage

Gao et al. [51] reported that under high temperature and low humidity midday depression of photosynthesis could occur in spring, summer, and autumn, and it occurred easily at the grain-filling stage in field-grown and pot-grown soybean plants. It is not clear, however, why midday depression occurs easily at this stage. There is a possibility that at this stage a particular microclimate around soybean plants or a combination of light, temperature, and water factors, leads easily to midday depression.

F. Circadian Rhythm

Many studies have shown that midday depression is not related to circadian rhythm. Under simulated habitat conditions in a growth chamber, increasing atmospheric stress in the form of higher temperature and lower humidity resulted in midday depression of transpiration rate and net photosynthetic rate of the leaves in *Arbutus unedo* and *Quercus ilex* due to midday stomatal closure, while midday depression did not occur when the atmospheric stress was absent. These experiments were carried out under the same light conditions on four consecutive days [38]. It was demonstrated by experiments in which only one environmental variable changed at a time while all others were held constant that a circadian component was not essential for the development of midday depression in *A. unedo* L. [13]. Obviously, the fluctuation in atmospheric conditions rather than circadian rhythm is responsible for midday depression.

Under constant conditions net photosynthetic rate in peanut (*Arachis hypogaea*) leaf displayed a rhythm change within a period of about 24 hr, but its valley value or depression was at midnight not at midday [52]. Gao et al. [53] reported that under relatively constant conditions of light, temperature, humidity, and CO_2 concentration, net photosynthetic rate and stomatal conductance were lower in the morning and afternoon, and higher around noon, indicating a periodic change, namely circadian rhythm. Nevertheless, the periodic change is not related to midday depression of photosynthesis observed in the field. Their experiments showed that midday depression of photosynthesis was negligible after soybean plants were transferred to relatively constant conditions from field conditions where they often displayed a remarkable midday depression. This fact indicates that under natural conditions the environmental factors rather than circadian rhythm are the determinants for the daily pattern of photosynthesis.

There is another view on the relationship between midday depression and circadian rhythm. On the basis of a remarkable midday depression of photosynthesis in rice plant observed under constant light and temperature conditions, Deng and Chen [54] concluded that midday depression is related to circadian rhythm. However, it is not clear whether air humidity around rice plants was constant during their observation.

V. BIOCHEMICAL FACTORS RESPONSIBLE FOR MIDDAY DEPRESSION

A. Photosynthate Accumulation

In 1868 Boussingault [55] first proposed a hypothesis that the accumulation of assimilates in an illuminated leaf might result in a reduction in net photosynthetic rate. Some investigators are in favor of the hypothesis and consider the photosynthate accumulation to be an important cause of the midday depression of photosynthesis [56]. Nevertheless, some studies have indicated that photosynthate accumulation has no negative effect on photosynthesis under normal conditions without environmental stress or block of assimilate export from leaves [12,57]. Moreover, it has been observed that the photosynthate content in wheat leaves is not higher during midday depression than in the morning when photosynthesis is actively going on. Net photosynthetic rate in wheat leaves decreased by less than 10% even when photosynthate contents were much higher than the control after blocking of photosynthate export from the leaves for 6 hr by heat girdling of the leaf sheath [20]. Undoubtedly, the effect should be even less when photosynthate export is normal. Therefore, photosynthate accumulation is not a likely cause of midday depression.

B. Decrease in Rubisco Activity

Rubisco is a key enzyme in photosynthetic carbon assimilation. It often limits the maximal net photosynthetic rate [58–60]. However, there is a great deal of evidence indicating that plants may contain excess Rubisco and that photosynthesis may be controlled by several enzymes or processes [61]. Perhaps, the activated amount rather than the total amount of Rubisco often limits the maximal photosynthesis. In consonance with this supposition, a soybean cultivar with a higher net photosynthetic rate had a higher carboxylation efficiency and higher initial activity of RuBP carboxylation of Rubisco [62]. In addition, under unfavorable conditions net photosynthetic rate may be maintained by a greater concentration of Rubisco [63]. A midday decline in carboxylation efficiency, namely, the initial slope of the A–C_i curve, associated with midday depression of photosynthesis has been observed in *Q. suber* leaves [37,64]. Furthermore, Jiang et al. [65] reported that midday depression of net photosynthetic rate was accompanied by a midday decline of Rubisco initial activity in rice flag leaves. It seems that midday depression is related to a decrease in Rubisco activity or content of activated Rubisco. However, one cannot be sure whether the decreased Rubisco activity is the main reason for midday depression of photosynthesis because of the lack of data on diurnal variation in stomatal conductance and intercellular CO_2 concentration measured simultaneously.

C. Enhanced ABA Biosynthesis

There is a possibility that abscisic acid (ABA) is an important biochemical factor responsible for midday depression. In the daily course of ABA content change, a midday peak associated with midday stomatal closure was observed in grape (*Vitis vinifera*) leaves [66]. Unfortunately, the diurnal variation in net photosynthetic rate was not measured simultaneously in this study. Thus, the relationship between ABA and midday depression of photosynthesis is still an open question.

D. Decline in Photosystem II Photochemical Efficiency

On clear days the midday decline in photosynthetic efficiency, expressed in apparent quantum yield of CO_2 uptake or chlorophyll fluorescence parameter F_v/F_m, a measure of phostosystem II (PS II) photochemical efficiency. often occurs in plants [67–70]. Naturally, the question arises whether the midday depression of net photosynthetic rate often observed results from the midday decline in photosynthetic efficiency.

Demmig-Adams et al. [3] observed that the midday depressions of net photosynthetic rate and stomatal conductance were accompanied by decreases in F_v/F_m and apparent quantum yield of O_2 evolution in *A. unedo* leaves. However, they were not sure whether this reduction in photochemical efficiency is serious enough to limit CO_2 fixation in high light and thereby to impose a nonstomatal limitation to net CO_2 uptake in *A. unedo* in the field at noon.

It should be pointed out that midday depression of the photosynthetic rate is always observed at saturating light, while the photosynthetic quantum efficiency is often measured at low light intensity. Therefore, decreased efficiency does not necessarily lead to a decrease in light-saturated rate because strong sunlight may compensate for the decline in PS II efficiency to maintain the high rate to some extent. The light-saturated rate of photosynthesis began to decrease when photoinhibition reached a level of 40% to 60%, and at a lower inhibition level the efficiency, but not the light-saturated O_2 production, was affected [71,72]. In wheat flag leaves a midday decline in photosynthetic efficiency was not invariably accompanied by midday depression of net photosynthetic rate. Intercellular CO_2 concentration decreased when midday depression of both the efficiency and the rate occurred simultaneously. Furthermore, photosynthetic rate was correlated with stomatal conductance and intercellular CO_2 concentration to a higher level of significance than with photosynthetic efficiency. These facts indicate that midday decline of photosynthetic efficiency may be, if at all, a less important cause of midday depression of net photosynthetic rate than midday closure of stomata in the case studied [41].

Some woody plants require a lower light intensity (a photon flux density not more than one half of full sunlight) to saturate photosynthesis. Thus, in these plants severe photoinhibition, characterized by a decrease in the quantum efficiency of photosynthetic carbon assimilation and a decline in PS II photochemical efficiency caused by excessive light energy, often occurs around noon on clear days. For these plants the main immediate cause of midday depression may be the decline in PS II photochemical efficiency induced by strong sunlight. In summer, midday depression of both the efficiency and the rate often occurred in the upper leaves of the bamboo canopy, while intercellular CO_2 concentration declined first, and then increased. These facts indicate that midday depression of net photosynthetic rate is related to decline in photochemical efficiency, at least in part [14]. Similarly, midday depression of net photosynthetic rate was accompanied by a pronounced decrease in leaf conductance and a substantial increase in intercellular CO_2 concentration, as well as a considerable decline in PS II photochemical efficiency (F_v/F_m) in *P. acaulos* [15]. Midday depression in tea (*Camellia sinensis*) [11] and grapevine (*Vitis uinifera*) [73] leaves has been attributed to photoinhibition. Results from other studies also show that photoinhibition may be a factor contributing to midday depression of photosynthesis [4,74].

As mentioned above, midday depression of net photosynthetic rate is closely related to many factors such as stomatal partial closure, decreased Rubisco activity, and declined PS II photochemical efficiency. Then, which of them, stomatal or nonstomatal factor, is the main cause of midday depression when these factors exist simultaneously? The data of change in intercellular CO_2 concentration (C_i) during midday depression may help to answer this question. In general, stomatal partial closure or a decrease in stomatal conductance may lead to a decreased C_i, whereas the decline in photosynthetic activity of leaf mesophyll cells such as a decrease in Rubisco carboxylation activity or PS II photochemical efficiency may induce an increase in C_i. The direction, increase or decrease, of change in C_i depends on the predominant one when changes in these factors occur simultaneously. When the decreases in stomatal conductance, Rubisco activity, and PS II photochemical efficiency occur simultaneously during midday depression, for example, if C_i declines, the main cause of midday depression is the decreased stomatal conductance. On the contrary, if C_i increases, the main cause must be the decreases in Rubisco activity and PS II photochemical efficiency. In this case, the direction rather than the extent of change in C_i is important for making the conclusion [75].

E. Possible Mechanisms

From most of the evidence cited above, it is suggested that for midday depression of photosynthesis, strong sunlight, low air humidity or high VPD, and low soil water potential may be the main environmental factors, decreased stomatal conductance may be the most important physiological factor, and increased ABA synthesis and decreased PS II photochemical efficiency may be the most important biochemical factors. Of course, these factors are closely linked to each other. Strong sunlight causes an increase in air temperature and a decrease in air relative humidity and soil water potential because of enhanced plant transpiration. These changes in ecological factors result in variations in the physiological and biochemical factors. Low soil water potential leads to increase in ABA synthesis, and both increased ABA and increased VPD cause a decrease in stomatal conductance, resulting in a decline in net photosynthetic rate due to decreased CO_2 supply. However, midday closure of stomata is not the sole important physiological or biochemical cause of midday depression. In some woody plants such as bamboo and tea, the decline in PS II photochemical efficiency induced by strong sunlight may be the most important biochemical cause of midday depression. Perhaps the main immediate cause and mechanism of midday depression are different for different plant species under various conditions. The factors related to midday depression are shown in Figure 16.2 [76,77].

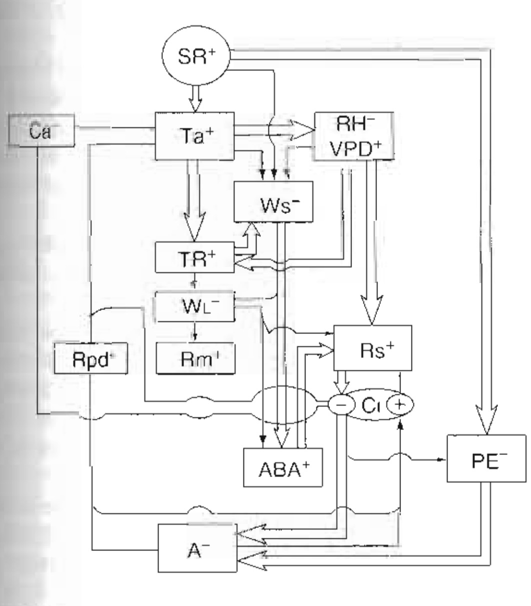

FIGURE 16.2 Possible relationships between ecological, physiological, and biochemical factors and midday depression. SR, solar radiation; Ta, air temperature; Ca, CO_2 concentration in the air; RH, relative humidity; VPD, water vapor pressure deficit from leaf cell to air; Ws, soil water potential; TR, transpiration; W_L, leaf water potential; Rpd, photorespiration and respiration; Rm, mesophyll resistance to CO_2 diffusion; Ci, CO_2 concentration in intercellular space; PE, photochemical efficiency; ABA, abscisic acid; A, net photosynthetic rate. "+" and "−" indicate increase and decrease, respectively. Double-line arrow indicates a strong effect.

VI. ADAPTIVE IMPORTANCE

A. Adaptive Importance

In many cases midday depression of photosynthesis seems to be a strategy to cope with environmental stresses formed during evolution. Midday stomatal closure and downregulation of photochemical efficiency are effective ways to avoid excess water loss and photodamage of the photosynthetic apparatus under strong sunlight and dry conditions.

Midday stomatal closure may be a response to low air humidity or high VPD. In this case midday closure of stomata is an important physiological cause of midday depression of photosynthesis. Alternately, midday closure of stomata may be a response to increased intercellular space CO_2 concentration due to a decline in mesophyll photosynthetic activity or increase in respiration and photorespiration. In this case midday closure of stomata is the result rather than the cause of decreased photosynthetic rate. In any case, midday stomatal closure always increases the water use efficiency of plants [78–80]. This is because of the predominant occurrence of leaf gas exchange in the morning and in the afternoon when net photosynthetic rate is higher and transpiration rate is lower. Obviously, such stomatal regulation is quick, reversible, and favorable for growth and development of plants under dry conditions of air and soil.

Downregulation of photochemical efficiency around noon is often observed in many plants under field conditions on clear days [69,81]. In some cases it may be responsible for the midday depression, for example, in the leaves of some woody plants such as bamboo and tea. Such downregulation may be due to enhanced thermal energy dissipation related to the xanthophyll cycle or the reversible inactivation of PS II, which is considered to be an important mechanism to protect the photosynthetic apparatus from photodamage [82–84]. Although there have been many studies, the molecular mechanism of such thermal energy dissipation is not yet clear [85–87].

B. Measure of Alleviation

Midday depression of photosynthesis, as a regulation process, is advantageous for the survival of plants under stress conditions, but it is at the expense of effective use of light energy and plant productivity. Midday depression may decrease crop productivity by 30% to 50% or more. Therefore, it is worthwhile to search for alleviating or eliminating measures. Under strong-light and high-transpiration conditions, midday mist irrigation could increase stomatal conductance and photosynthetic rate in leaves of *Beta vulgaris* despite adequate soil water supply [88]. Mist irrigation for 40 days not only increased the photosynthetic rate in cassava leaves but also increased production of dry roots (91%) and total biomass (27%) [89]. Similar effects of mist irrigation were observed in wheat and soybean plants. Mist irrigation in the grain-filling period increased stomatal conductance and net photosynthetic rate in flag leaves, thus increasing grain yield by about 18% in wheat [32]. Mist irrigation in the seed-filling period increased the seed yield by about 19% in soybean [10].

VII. CONCLUDING REMARKS

Midday depression of photosynthesis is a common phenomenon in higher plants. It is related to many external and internal factors interacting with each other. Midday stomatal closure or decreased photochemical efficiency may cause the midday depression, depending on plant species and environmental conditions. It may be a strategy of plants to cope with environmental stresses. Further study on the mechanisms of midday depression is required for understanding the regulation of photosynthesis and finding ways to increase plant productivity. Because the present viewpoints and hypotheses about these mechanisms are based on inadequate or incomplete data, in the following studies a better combination of many kinds of experimental methods, such as physiological, biochemical, and biophysical ones, is absolutely necessary for getting more abundant data to reveal exactly these mechanisms.

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