Chapter 12
Effects of Physical Environment on Photosynthesis, Respiration, and Transpiration

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Abstract Responses of photosynthetic, respiratory, and transpiration rates of plants to the levels of physical environmental factors are outlined. Water vapor movement from a leaf to the atmosphere in transpiration is quantitatively described using a gas diffusion model that incorporates the concentration gradient of water vapor and the conductance for water vapor. Changes in the levels of environmental factors affect transpiration rate directly through changes in the driving force of water vapor diffusion or indirectly through changes in stomatal aperture. In plants, there are two types of respiration, namely, dark respiration and photorespiration, although they are completely different metabolisms. Dark respiratory rate is sensitive to changes in temperature, gas concentrations, and light intensity, and the effects are summarized. Photosynthetic carbon dioxide (CO_2) influx of a leaf is spatially divided into CO_2 diffusion from the atmosphere to the chloroplasts and biochemical CO_2 fixation within the chloroplasts. The former can be described with a model in a similar manner to that for water vapor diffusion. Net photosynthetic rate in C_3 leaves shows a saturating-type increase in response to increases in CO_2 concentration or photosynthetic photon flux density (PPFD), and the response curves are characterized by several parameters. Net photosynthetic rate is low at extremely low and high temperatures and shows an optimum level at intermediate temperatures.

Keywords CO_2 diffusion • Conductance • Environmental factor • Flux • Response curve • Stomata • Water vapor diffusion

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12.1 Introduction

Photosynthesis, respiration, and transpiration are fundamental physiological processes of plants and are closely associated with their growth and development. The reaction rates of these processes are largely influenced by the environment of the plant. On the other hand, through these processes, energy and compounds such as water vapor and CO_2 are exchanged between the plant and the surrounding atmosphere, which thereby affects the environment. Understanding this plant–environment interaction is important for controlled environment agriculture in order to attain optimal facility design and operation as well as appropriate plant management practices.

In this chapter, I present an outline of the environmental effects on photosynthesis, respiration, and transpiration of green plants. An environmental factor can be categorized on the basis of its characteristics into the physical, chemical, or biological environment. Here I focus on the physical environment, which includes the light, thermal, humidity, and gas environments. I consider only C_3 photosynthesis and not C_4 and crassulacean acid metabolism (CAM) photosynthesis, because most plant species currently grown in greenhouses and plant factories with artificial lighting (PFAL) are C_3 plants. Refer to Chap. 8 for the physiological basis of photosynthesis and transpiration as well as the light spectral effects on photosynthesis.

12.2 Transpiration

Transpiration of leaves drives the transpiration stream in the xylem and therefore water and nutrient uptake by roots. Regulation of transpiration rate at appropriate levels by environmental control in greenhouses and PFAL is thus important to maintain a favorable water and nutritional status of the plants. Transpiration also contributes to dissipation of energy absorbed by leaves into the atmosphere in the form of latent heat. I introduce this section with a model describing water vapor diffusion from the leaf to the atmosphere and then summarize the effects of environmental factors on transpiration rate, particularly in relation to stomatal responses.

12.2.1 Water Vapor Diffusion Model

Figure 12.1 shows a schematic diagram of water vapor and CO_2 diffusion between a leaf and the atmosphere. Water vapor in the intercellular air spaces, which has evaporated at the mesophyll cell surface, diffuses to the atmosphere immediately external to the leaf through stomatal pores surrounded by guard cells. Water vapor

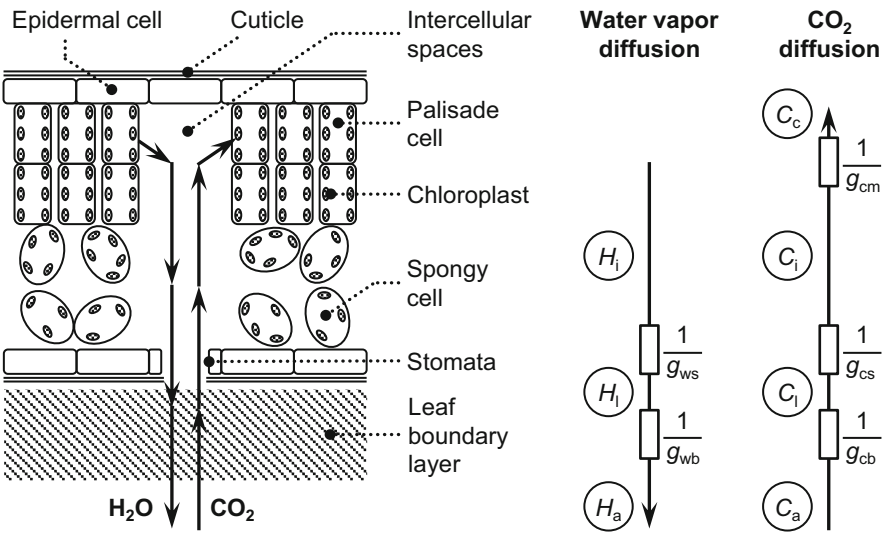

Fig. 12.1 Schematic diagram of cross-sectional view of a dorsiventral leaf (*left*) and models of water vapor and CO_2 diffusion between the leaf and the atmosphere with diffusion resistance (the inverse of conductance) between them (*right*). Cuticular transpiration is omitted. H_i, H_l, and H_a: mole fractions of water vapor in the intercellular air spaces, immediately external to the leaf surface, and in the atmosphere beyond the leaf boundary layer; g_{ws} and g_{wb}: stomatal and leaf boundary layer conductances for water vapor; C_a, C_l, C_i, and C_c: mole fractions of CO_2 in the atmosphere, immediately external to the leaf surface, in the intercellular spaces, and in the hypothetical air equilibrated with the chloroplast stroma; g_{cb}, g_{cs}, and g_{cm}: leaf boundary layer, stomatal, and mesophyll conductances for CO_2

diffuses further to the free atmosphere through the leaf boundary layer. Water vapor or liquid water also moves across the cuticle layer on the leaf epidermis, but the extent is substantially lower than that through stomata and thus is ignorable in most cases. Water vapor diffusion can be quantitatively described on the basis of an analogy of Ohm's law. By this principle, transpiration rate per unit leaf area, T [molH_2O m^{-2} s^{-1}], is proportional to the difference in mole fractions of water vapor at given two representative points. Conductance is the inverse of resistance and is often used instead of resistance in the model. T at a steady state is expressed as:

$$T = g_{wt}(H_i - H_a) \tag{12.1}$$

where H_i and H_a [mol mol^{-1}] are the respective mole fractions of water vapor in the intercellular air spaces and in the atmosphere beyond the leaf boundary layer, and g_{wt} [molH_2O m^{-2} s^{-1}] is the total water vapor conductance between them. The g_{wt} is divided into stomatal conductance, g_{ws} [molH_2O m^{-2} s^{-1}], and leaf boundary layer conductance, g_{wb} [molH_2O m^{-2} s^{-1}], for water vapor:

$$\frac{1}{g_{\mathrm{wt}}} = \frac{1}{g_{\mathrm{ws}}} + \frac{1}{g_{\mathrm{wb}}}$$
$$g_{\mathrm{wt}} = \frac{g_{\mathrm{ws}} g_{\mathrm{wb}}}{g_{\mathrm{ws}} + g_{\mathrm{wb}}} \tag{12.2}$$

where g_{ws} and g_{wb} are connected in series. Using g_{ws} and g_{wb}, T at a steady state is also written as:

$$T = g_{\mathrm{ws}}(H_{\mathrm{i}} - H_{\mathrm{l}}) = g_{\mathrm{wb}}(H_{\mathrm{l}} - H_{\mathrm{a}}) \tag{12.3}$$

where H_{l} [mol mol^{-1}] is the mole fraction of water vapor immediately external to the leaf surface.

Changes in the levels of environmental factors affect T directly and/or indirectly. The former is the effect on the concentration gradient of water vapor. The latter, on the other hand, is the effect on T through alterations of g_{wb} and/or g_{ws}. For example, g_{wb} decreases with increasing thickness of the leaf boundary layer, and the thickness is influenced by wind speed as well as leaf morphological characteristics (Campbell and Norman 1998; refer also to Chap. 13). Changes in a variety of environmental factors cause a rapid response of g_{ws} within seconds to minutes. Alteration of g_{ws} influences not only T but also photosynthetic CO_2 assimilation, the regulation of which is important for carbon gain by plants (see Sect. 12.4.1).

12.2.2 *Effects of Humidity*

Humidity directly affects T. Let us consider the effect quantitatively using Eq. 12.1. In general, the mole fraction of water vapor in the intercellular air spaces, H_{i}, can be assumed to be saturated at the leaf temperature, t_{l} [°C]:

$$H_{\mathrm{i}} = \frac{e_{\mathrm{s}}(t_{\mathrm{l}})}{p} \tag{12.4}$$

where $e_{\mathrm{s}}(t_{\mathrm{l}})$ [Pa] is the saturated water vapor pressure at t_{l}, and p is the atmospheric pressure [Pa]. Equation 12.1 is then rewritten using the atmospheric water vapor pressure, e [Pa]:

$$T = g_{\mathrm{wt}}(H_{\mathrm{i}} - H_{\mathrm{a}}) = \frac{g_{\mathrm{wt}}(e_{\mathrm{s}}(t_{\mathrm{l}}) - e)}{p} \tag{12.5}$$

where $(e_{\mathrm{s}}(t_{\mathrm{l}}) - e)$ is termed the leaf-to-air water vapor pressure deficit (VPD). It is clear from this equation that, if the total water vapor conductance (g_{wt}) and p are constant, T is proportional to leaf-to-air VPD. Leaf-to-air VPD is thus more appropriate than relative humidity (the percentage of e to e_{s} at the air temperature) when evaluating the effect of humidity on T.

Humidity also affects *T* indirectly via a change in stomatal conductance: stomata tend to close when leaf-to-air VPD is high. Stomatal conductance and consequently total water vapor conductance decrease in order to suppress excessive water loss. Such the decrease in stomatal conductance thus counteracts the direct effect of high leaf-to-air VPD on *T*.

12.2.3 Effects of Rhizosphere Environment

Moisture deficiency and excess salt accumulation in the rhizosphere, which potentially cause water stress in plants, are typical stimuli that trigger stomatal closure. The phytohormone abscisic acid is known to be a chemical inducer of stomatal closure. Abscisic acid is generated in roots in response to water shortage, is transported to leaves via the xylem sap, and induces stomatal closure. The rapid decrease in stomatal conductance triggered by this mechanism, before any negative impacts of water deficiency are experienced, is considered to be a kind of feedforward response of plants, which should prevent subsequent excess water loss (Lambers et al. 2008).

12.2.4 Effects of Light Intensity and Spectrum

Stomatal conductance increases with increasing PPFD (Fig. 12.2a), thus promoting transpiration (Fig. 12.2b). This response facilitates CO_2 uptake for photosynthesis under high PPFD conditions as well as evaporative cooling of the leaf subjected to a high radiative heat load. The light-driven response of stomata occurs via at least two mechanisms (Shimazaki et al. 2007). One is the blue light (BL)-dependent response, mediated by the BL photoreceptor phototropin. The extent of response is considered to be saturated by a relatively low BL intensity. The other mechanism is the photosynthesis-dependent response, which is thought to be driven by the photosynthetic activity of mesophyll cells and/or guard cells, although the details of the mechanism remain unclear.

12.2.5 Effects of CO_2 Concentration

Stomatal conductance tends to increase at low CO_2 concentrations and decrease at high CO_2 concentrations. Such changes in stomatal conductance in response to CO_2 concentration play a role in compensating in part for the altered photosynthetic rate, which is directly affected by CO_2 concentration (see Sect. 12.4.2). The response to high CO_2 concentration also contributes to reduction in water loss relative to CO_2 uptake through stomata. The photosynthetic water-use efficiency, defined as the

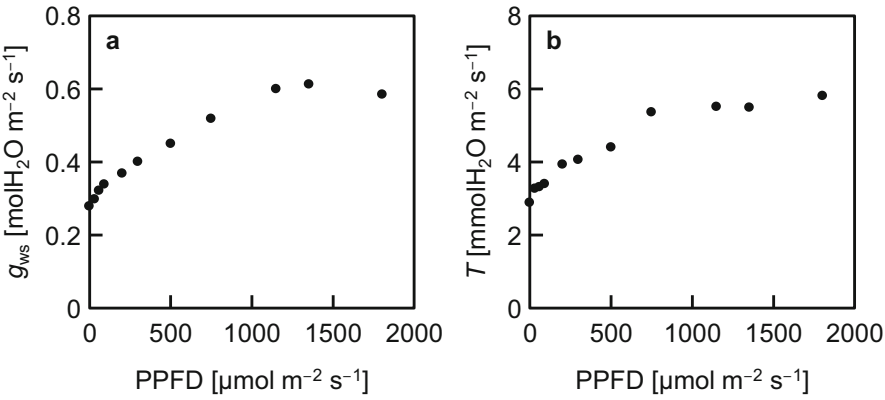

Fig. 12.2 Stomatal conductance for water vapor (g_{ws}, **a**) and transpiration rate (T, **b**) at different incident PPFDs in a spinach leaf (Matsuda et al. unpublished). Measurements were made at an atmospheric CO_2 concentration of 360 μmol mol^{-1}, a leaf temperature of 25 °C, and a leaf-to-air water vapor pressure deficit of 1.1 kPa. Light was provided by a white halogen lamp

ratio of net photosynthetic rate to T, both expressed on a leaf area basis (Lambers et al. 2008), therefore increases at high CO_2 concentrations.

12.2.6 Effects of Temperature

Because leaf-to-air VPD is a function of leaf temperature (Eq. 12.5), leaf temperature affects T. On the other hand, a change in leaf temperature causes alterations in photosynthetic and respiratory rates (see Sects. 12.4.4 and 12.3.2, respectively), which may indirectly affect T through changes in stomatal conductance. Moreover, an increase in T leads to a reduction in leaf temperature via latent heat loss of leaves. Thus, there is a complex interrelationship between leaf temperature and T. At a steady state, leaf temperature and T are determined so that the energy budget of the leaf balances. Refer to Campbell and Norman (1998) and Jones (2014) for detailed description of the leaf energy balance.

12.3 Respiration

12.3.1 Dark Respiration and Photorespiration

In plants, there are two types of the so-called respiration, namely, dark respiration and photorespiration, although they are completely different metabolisms. The pathway of dark respiration consists of the glycolysis and pentose phosphate pathway located in the cytosol and the plastids, followed by the tricarboxylic acid

cycle and oxidative phosphorylation in the mitochondria. The role of dark respiration is to provide chemical energy and reducing power by oxidizing respiratory substrates such as carbohydrates, as well as provide intermediate metabolites as materials for a variety of biological compounds. Photorespiration is a metabolism specific to photosynthetic organisms and is localized in the chloroplasts, peroxisomes, and mitochondria. A role of the photorespiratory pathway is to minimize carbon loss that results almost inevitably from O_2 fixation in the Calvin cycle located in the chloroplasts. Photorespiration is observed only in photosynthetic organs, whereas dark respiration basically proceeds in every plant organ.

In spite of the metabolic differences, plants uptake O_2 and release CO_2 through both dark respiration and photorespiration. Dark respiration occurs both in the light and the dark, whereas photorespiration proceeds only in the presence of incident light. Therefore, when the rate of CO_2 efflux is measured without light irradiation, whereby neither photosynthesis nor photorespiration is active, the efflux rate corresponds to dark respiratory rate. It should be noted, however, that dark respiratory rate is reported to be influenced by the light environment (see Sect. 12.3.4).

12.3.2 Effects of Temperature

The dark respiratory rate of plant organs is sensitive to temperature. The rate increases almost exponentially with increasing temperature between approximately 10 and 40 °C (Fig. 12.3), although the extent of increase varies among species and growth conditions. Such temperature dependence of dark respiratory rate is often expressed using the Q_{10} model. According to the model, dark respiratory rate per unit area, R_d [molCO_2 m^{-2} s^{-1}], at an organ/plant temperature of t_p [°C] is expressed as:

$$R_d = R_{ref} Q_{10}{}^{t_{dif}} \tag{12.6}$$

where

$$t_{dif} = \frac{t_p - t_{ref}}{10} \tag{12.7}$$

R_{ref} [molCO_2 m^{-2} s^{-1}] is R_d at a reference temperature, t_{ref} [°C]. The Q_{10} value for plant R_d is approximately 2 (Lambers et al. 2008), which means that a 10 °C increase in temperature brings about a twofold increase in R_d.

Suppression of R_d by decreasing temperature is employed for storage of postharvest fruits, vegetables, cut flowers, and sometimes seedlings. On the other hand, over-suppression of R_d of growing plants by lowering temperature at night is not necessarily effective for promoting growth because of the importance of dark respiration in the construction of new tissues and organs.

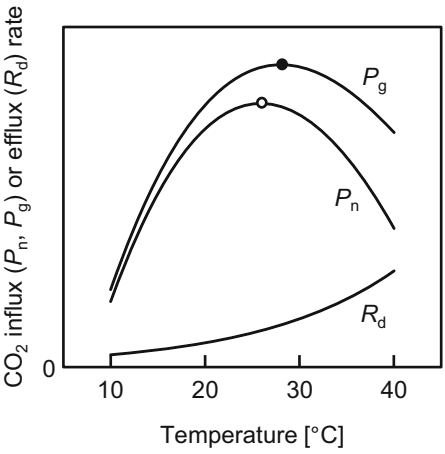

Fig. 12.3 Schematic diagram of responses of net (P_n) and gross (P_g) photosynthetic rates and dark respiratory rate (R_d) to temperature in a C_3 leaf. P_n and P_g: cubic functions; R_d: the Q_{10} model (Sect. 12.3.2). Open and filled circles represent the maximal values for P_n and P_g, respectively

12.3.3 Effects of O_2 and CO_2 Concentrations

Decrease in O_2 concentration and elevation of CO_2 concentration tend to suppress R_d of plants. In greenhouses and PFAL, atmospheric O_2 concentration remains at the ambient level of 21 % and barely fluctuates and therefore has little effect on R_d of the aboveground parts of plants. On the other hand, CO_2 concentration is often enriched during the day for promotion of photosynthesis (see Sect. 12.4.2), but the concentration is generally too low to reduce R_d. In postharvest storage, O_2 and CO_2 concentrations around the harvested products can be decreased and increased, respectively, in order to suppress respiration and prolong storage life. In hydroponics, the dissolved O_2 concentration in the rhizosphere can sometimes decline below the level required for root respiration as a result of insufficient aeration.

12.3.4 Effects of Light Intensity

Several studies have shown that R_d of leaves is influenced by light intensity (Brooks and Farquhar 1985): the estimated rate in the light is significantly lower than the measured rate in the dark for the same leaf. Moreover, the rate drastically decreases as the light intensity increases. For distinction, dark respiration under incident light is sometimes referred to specifically as “day” respiration.

12.4 Photosynthesis

Photosynthesis consists of a series of reactions by which CO_2 is assimilated using light energy for carbohydrate synthesis and is thus an important physiological function that directly influences plant growth and yield. The reactions proceed in the chloroplasts. The net photosynthetic rate per unit leaf area, P_n [molCO_2 m^{-2} s^{-1}], is expressed as:

$$P_n = P_g - R_d \tag{12.8}$$

where P_g [molCO_2 m^{-2} s^{-1}] is gross photosynthetic rate per unit leaf area. In this chapter, photorespiratory CO_2 efflux is included in P_g.

Photosynthetic CO_2 influx of a leaf can spatially be divided into two processes: CO_2 diffusion from the atmosphere to the chloroplasts and the biochemical CO_2 fixation inside the chloroplasts. In the following sections, the model of CO_2 diffusion from the atmosphere to the chloroplasts is first described. Then, the effects of the physical environment on P_n are summarized. In this chapter, I mainly focus on leaf photosynthesis. Responses of canopy photosynthesis to environmental changes often differ from those of leaf photosynthesis. Several characteristics of canopy photosynthesis are discussed in Chaps. 9 and 13.

12.4.1 CO_2 Diffusion Model

Diffusion of CO_2 from the atmosphere to the chloroplasts can be described in a similar manner to that for water vapor diffusion, although water vapor and CO_2 diffusion occur in opposite directions in a photosynthesizing leaf (Fig. 12.1). Because of resistance against CO_2 diffusion, as observed for water vapor diffusion, the CO_2 concentration in the intercellular air spaces of the leaf may be as low as approximately 70 % of that in the atmosphere (Evans and Loreto 2000). Although water vapor in the intercellular spaces is considered to be equilibrated with liquid water in the mesophyll cells, CO_2 gas in the intercellular spaces is dissolved in the liquid of mesophyll cells and further diffuses to the chloroplast stroma against an additional resistance.

Calculation of P_n at a steady state is written as follows:

$$\begin{aligned} P_n &= g_{ct}(C_a - C_c) \\ &= g_{cb}(C_a - C_l) = g_{cs}(C_l - C_i) = g_{cm}(C_i - C_c) \end{aligned} \tag{12.9}$$

where C_a, C_l, C_i, and C_c [mol mol^{-1}] are the respective mole fractions of CO_2 in the atmosphere, immediately external to the leaf surface, in the intercellular spaces, and in the hypothetical air equilibrated with the chloroplast stroma. The g_{ct} [molCO_2 m^{-2} s^{-1}] is the total CO_2 conductance between the atmosphere and the chloroplast

stroma, consisting of three conductances connected in series. Leaf boundary layer conductance, g_{cb} [molCO_2 m^{-2} s^{-1}], and stomatal conductance, g_{cs} [molCO_2 m^{-2} s^{-1}], for CO_2 are analogous to those for water vapor. Mesophyll conductance (or internal conductance) for CO_2, g_{cm} [molCO_2 m^{-2} s^{-1}], is the additional conductance, present between the mesophyll cell surface and the chloroplast stroma. Several anatomical and biochemical properties of leaves are reportedly involved in g_{cm} (Evans and Loreto 2000).

The conductance for water vapor and CO_2 can be converted into each other using the conductance ratio in the still air for stomatal conductance and that in the laminar flow for boundary layer conductance, respectively (Farquhar and Sharkey 1982):

$$g_{ws} = 1.6 g_{cs} \tag{12.10}$$

$$g_{wb} = 1.37 g_{cb} \tag{12.11}$$

Changes in stomatal conductance in response to changes in the levels of environmental factors, as seen in Sects. 12.2.2, 12.2.3, 12.2.4, 12.2.5, and 12.2.6, therefore potentially influence P_n via CO_2 diffusion. For example, regulation of leaf-to-air VPD at a low level contributes to maintaining a high degree of stomatal opening (Sect. 12.2.2), thereby promoting CO_2 diffusion into the leaf.

12.4.2 *Effects of CO_2 Concentration*

In general, P_n in C_3 leaves shows a saturating-type increase in response to increasing CO_2 concentration (Fig. 12.4). The increment of P_n gradually decreases as CO_2 concentration increases, and P_n does not increase further once CO_2 concentration increases beyond a certain critical level. The latter CO_2 concentration is termed the CO_2 saturation point (CSP). The CO_2 compensation point (CCP), on the other hand, is the CO_2 concentration at which P_n is zero. In Fig. 12.4a, P_n is plotted against atmospheric CO_2 concentration (C_a), but a similar trend is also observed when P_n is plotted against intercellular CO_2 concentration (C_i) (Fig. 12.4b), which mostly reflects the CO_2 fixation characteristics at the chloroplast level. The C_i-response curve of P_n is referred to as the demand function, whereas Eq. 12.9 (dashed line in Fig. 12.4b) is referred to as the supply function (Farquhar and Sharkey 1982). The actual P_n of a leaf at a given external CO_2 concentration is determined from the intersection of the two lines.

Enrichment of CO_2 is frequently employed in greenhouses and PFAL in order to increase P_n and thereby biomass production. For example, CO_2 concentration can be approximately doubled in greenhouses and increased to 1,000–2,000 μmol mol^{-1} in PFAL. Indeed, P_n is increased initially in accordance with the CO_2-response curve of P_n. Note, however, that the extent of increase in P_n sometimes gradually decreases when a high CO_2 concentration is maintained and prolonged (the downregulation of photosynthesis).

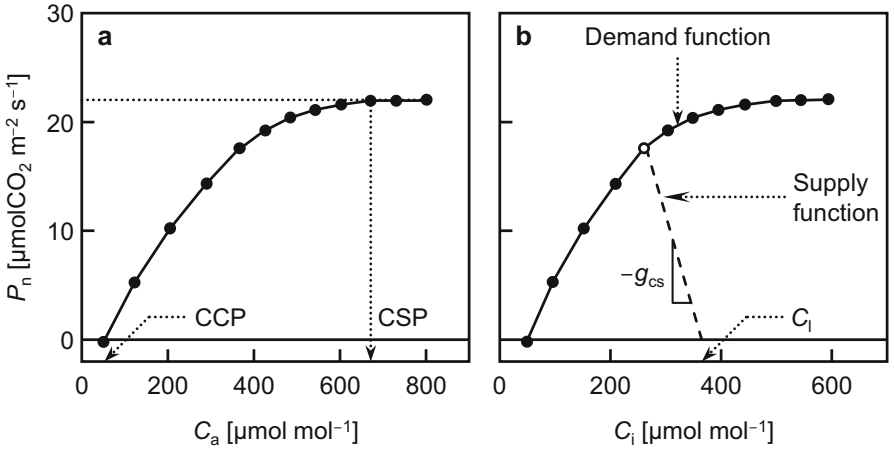

Fig. 12.4 (**a**) Net photosynthetic rate (P_n) at different atmospheric CO_2 concentrations (C_a) in a tomato leaf (Matsuda et al. unpublished). Measurements were made at a PPFD of 1,500 μmol m^{-2} s^{-1}, a leaf temperature of 25 °C, and a leaf-to-air water vapor pressure deficit of 1.1 kPa. Light was provided by blue and red LEDs. CCP: CO_2 compensation point; CSP: CO_2 saturation point. (**b**) P_n as a function of intercellular CO_2 concentration (C_i). Dashed line: the supply function [$P_n = g_{cs}(C_l - C_i) = -g_{cs}(C_i - C_l)$, where $g_{cs} = 1.66$ molCO_2 m^{-2} s^{-1} and $C_l = 367$ μmol mol^{-1}]; solid line: the demand function (C_i-response curve of P_n). The open circle represents the realized P_n and C_i of the leaf

12.4.3 Effects of Light Intensity

Figure 12.5 shows an example of the response of leaf P_n to PPFD. Under the dark conditions of 0 mol m^{-2} s^{-1} PPFD, P_n equals to $-R_d$. With increasing PPFD, P_n initially increases almost linearly. The increment of P_n gradually decreases with further increase in PPFD. Similarly to the CO_2-response curve, the light saturation point (LSP) and light compensation point (LCP) are defined as the PPFDs at which P_n becomes maximum and zero, respectively. The LSP of mature leaves is approximately 1,000–1,500 μmol m^{-2} s^{-1} for species favoring high PPFDs, such as tomato and cucumber, whereas it is in general less than 1,000 μmol m^{-2} s^{-1} for leafy vegetables. P_n measured at LSP, at a normal CO_2 concentration, and at an optimal leaf temperature is often referred to as the photosynthetic capacity of the leaf. It is well known that leaves grown under high PPFD ("sun" leaves) have higher LSP, LCP, photosynthetic capacity, and R_d than those grown under low PPFD ("shade" leaves). The initial slope of the curve at very low PPFDs reflects the maximal light-use efficiency for photosynthesis. When the efficiency is evaluated on an absorbed PPFD basis (i.e., the quantum yield of photosynthesis), the theoretical maximum for C_3 leaves is 0.125 mol mol^{-1} (1 mol of CO_2 is fixed per 8 mol of absorbed photons).

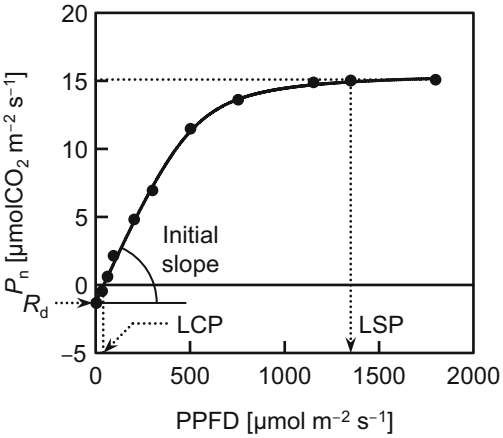

Fig. 12.5 Net photosynthetic rate (P_n) at different incident PPFDs in a spinach leaf (Matsuda et al. unpublished). Measurements were made at an atmospheric CO_2 concentration of 360 μmol mol^{-1}, a leaf temperature of 25 °C, and a leaf-to-air water vapor pressure deficit of 1.1 kPa. Light was provided by a white halogen lamp. R_d: dark respiratory rate; LCP: light compensation point; LSP: light saturation point

12.4.4 Effects of Temperature

The P_g and P_n are low at extremely low and high temperatures and show optimum levels at intermediate temperatures: the temperature dependences can thus be fitted with concave functions (Fig. 12.3). The optimal temperature for P_n is in general slightly lower than that for P_g because of the exponential increase in R_d with increasing temperature (Sect. 12.3.2).

In plants grown at higher temperatures, the optimal temperature for P_n is increased: it increases by 0.4–0.5 °C on average with an increase in growth temperature by 1 °C in C_3 leaves (Yamori et al. 2014). Several physiological and biochemical mechanisms are thought to be involved in this change in temperature dependence of P_n, which are being extensively studied.

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