Chapter 9
Optical and Physiological Properties of a Plant Canopy

Yasuomi Ibaraki

Abstract The characteristics of masses of leaves should be considered while controlling the light environment for plant production. The term "canopy" is used to express the mass of leaves of multiple plants. The optical characteristics and photosynthetic properties of a canopy are sometimes different from those of a single leaf. One of the most important characteristics of a canopy is that there exists a photosynthetic photon flux density (PPFD) distribution on and within the canopy according to its leaf distribution pattern. In addition, the light spectral distribution within the canopy is different from that outside the canopy, owing to light absorption and reflection by leaves. Moreover, the light-photosynthetic curve of a canopy differs from that of a single leaf, showing higher or no light-saturated points. A basic method for estimating canopy photosynthesis is to sum up the photosynthetic rates of small parts of canopy that are assumed to be under uniform environmental conditions. An extinction coefficient is used to express light attenuation within a canopy as a function of LAI and to estimate average PPFD at each horizontal layer.

Keywords Canopy photosynthesis • Extinction coefficient • Growth analysis • Leaf area • Light attenuation • Net assimilation rate • PPFD distribution • RGR

9.1 Introduction

As described in the previous chapter (Chap. 8), the optical and physiological properties of a plant leaf are important to understand the light environment needed for plant production. Note that plants have multiple leaves and only single plants are rarely cultivated in agricultural practice. Therefore, the characteristics of masses of leaves should be considered while controlling the light environment for plant production. The term "canopy" is used to express the mass of leaves of multiple plants. According to Moffett (2000), the term "canopy" is defined as the aboveground plant organs within a community. As plants grow, their biomass increases due to photosynthesis. Photosynthesis of a canopy/individual plant is

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the sum total of the photosynthesis of each leaf composing the canopy or plant. However, light environments differ among leaves owing to differences in the spatial positions in the canopy. In addition, a leaf's photosynthetic properties depend on the leaf's physiological states, including leaf age, water content, and environmental history. Thus, the process of summing the photosynthetic amounts of individual leaves over a canopy is complicated. In addition, note that the optical characteristics of a canopy are sometimes different from those of a single leaf. For example, the reflectance of a plant canopy tends to be rather lower than that of its components, i.e., single leaves, because multiple reflections between adjacent leaves and between leaves and stems lead to trapping of radiation (Jones 1992).

One of the most important characteristics of a canopy that should be considered in plant cultivation is that there exists a photosynthetic photon flux density (PPFD; μmol m^{-2} s^{-1}) distribution on and within the canopy according to its leaf distribution pattern. This PPFD distribution is critical for photosynthesis of the plant canopy and consequently affects growth. Proper understanding of PPFD distribution within/on a plant canopy is likely to be required in the application of artificial lighting for plant production.

Normally, the total leaf area of a plant canopy that has grown well is greater than the ground area below it. The ratio of the total leaf area to the ground area (which is referred to as the leaf area index (LAI); see Chap. 10 for details) depends on plant species, the growth stage, and cultivation density. The concept of LAI is useful when considering light distribution and canopy photosynthesis.

In this chapter, the optical and physiological properties of a plant canopy are introduced with the concept of extinction coefficients to express light attenuation as a function of LAI in order to understand the PPFD distribution in a canopy. Methods for estimating canopy photosynthesis will also be introduced.

9.2 Light Attenuation Through Plant Canopy

Light falling on a canopy surface enters the canopy and attenuates through absorption and reflection by leaves. Under the assumption of a horizontally uniform structure for the canopy, the vertical light distribution within canopy can be expressed by the following equations:

$$I = I_0 e^{-k \cdot F} \ \text{ or } \ \ln\left(\frac{I}{I_0}\right) = -k \cdot F, \tag{9.1}$$

where I is the irradiance (W m^{-2}) or photon flux density (μmol m^{-2} s^{-1}) at vertical position z from the top surface of the canopy, I_0 is the irradiance/photon flux density at the top of the canopy, F is the leaf area index summed from the top to z (which is sometimes referred to as cumulative LAI), and k is the extinction coefficient. This equation is analogous to Beer's law expressing light attenuation in a homogeneous
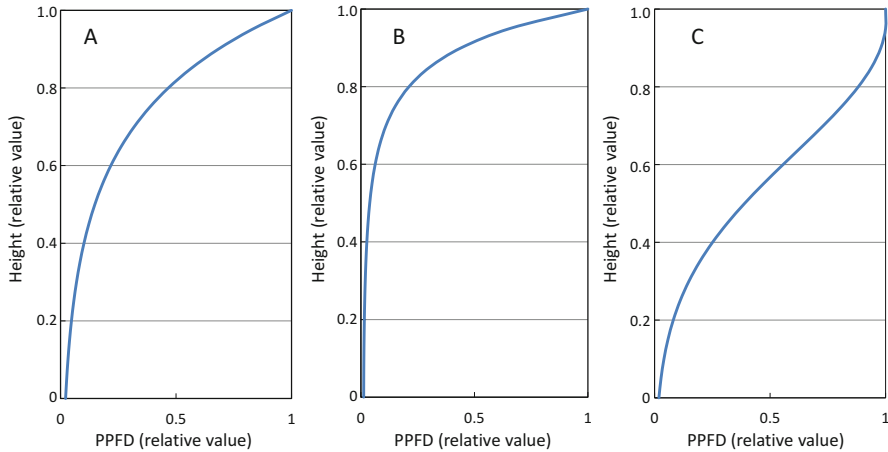
Fig. 9.1 Typical vertical PPFD distribution patterns within plant canopy depicted using Eq. 9.1 for canopies in which leaf area is distributed evenly (**a**), decreases linearly toward the *bottom* (**b**), and increases linearly toward the *bottom* (**c**)

medium and expresses the exponential attenuation of light as a function of vertically accumulated LAI within the canopy. The extinction coefficient depends not only on the leaf optical properties but also on the geometrical structure of the canopy, including the size, shape, and inclination of leaves, as well as on the azimuth and altitude of the sun. Figure 9.1 shows a typical PPFD distribution pattern within a plant canopy depicted using an Eq. 9.1 for a case in which light enters from the top of canopy.

The concept of considering the light distribution within a canopy as a function of LAI using the extinction coefficient has been commonly used for various types of plant canopies, in particular for forests and crops in which the plants have considerable height and there is a vertical leaf distribution, such as in orchards or cereal crops. In the case of leaf lettuce, which is a dominant species for cultivation in plant factories, the concept for vertical light distribution may be difficult to apply because it is difficult to define the horizontal multilayer due to its lower height or the leaf distribution pattern. However, note that there still is a variation in irradiance/photon flux density within the canopy or on the canopy surface even in such lower canopies.

9.3 Extinction Coefficients in Plant Canopy

Examples of extinction coefficients in various types of canopies are listed in Table 9.1. The extinction coefficients depend on the canopy structure and direction of incident light as described above. Although the differences among plant species is mainly due to differences in their canopy structures, note that for a given species,

Table 9.1 Examples of extinction coefficient k for PAR of various types of canopies

Type of canopy/species	Extinction coefficient k	Reference
Mainly horizontal leaves, such as sunflower or cotton	0.7–1.0	Fukai (1999)
Mainly erect leaves, such as barley and sugar cane	0.3–0.6	Fukai (1999)
Lettuce	*0.80, **0.66	*Javanovic et al. (1999)
		** Tei et al. (1996)
Onion	*1.06, **0.47	*Javanovic et al. (1999)
		**Tei et al. (1996)
Cabbage	1.17	Javanovic et al. (1999)

the structure may change with growth. For a given leaf area profile, large k values generally imply that photon irradiance (photon flux density) decreases rapidly with depth, whereas a canopy with a small k would allow solar radiation to penetrate deeply (Fukai 1999).

Under simple assumptions, k can be calculated. For example, in a canopy comprising only randomly distributed horizontal opaque leaves that can be divided into horizontal layers with the same leaf area without leaves overlapping, the extinction coefficient will be 1. As individual leaves are opaque in this case, the change in irradiance/photon flux density (dI) when light passes through a layer with LAI of dF is equal to $-I\,dF$:

$$dI = -I\,dF \tag{9.2}$$

where I is the irradiance/photon flux density at the top of the layer.

Integrating this relationship downward through total LAI gives the average irradiance/photon flux density on a horizontal surface below the position with that LAI (F):

$$I = I_0 e^{-F} \tag{9.3}$$

where I_0 is I at top layer (i.e., I when $F = 0$). Thus, $k = 1$ in this case.

For a canopy comprising leaves at other angles under the same assumptions, the extinction coefficient k is assumed to be the ratio of the shadow area to the actual leaf area. Thus, if the solar elevation angle is β, k equals $\cot \beta$ for vertical leaves and $\cos \alpha$ for leaves with an inclination angle of α (Fig. 9.2).

In real canopies, the distribution pattern of leaves is complicated and varies with time. Therefore, calculation of k is difficult without simple assumptions of leaf distribution. Examples of calculating k using simple leaf distribution models are described by Jones (1992).
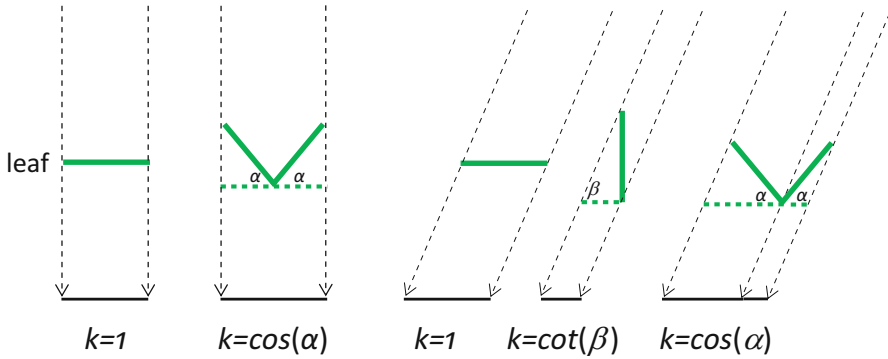
Fig. 9.2 Extinction coefficient k as the ratio of the shadow area to the actual leaf area for several cases under sun light. α is leaf inclination angle and β is the solar elevation angle

In contrast, k can be estimated for a real canopy based on light distribution measurements (Fig. 9.3).

As a more simple method, using measurements of irradiance/photon flux density I_0 above the canopy surface and I_n on the ground, k can also be estimated by the following equation:

$$k = -\frac{\ln\left(\frac{I_n}{I_0}\right)}{\text{LAI}}.$$

(9.4)

In this case, both the direction of incident light (solar elevation angle) and clumping index (a nonrandom spatial distribution parameter) are implicitly included in k, which implies that k may vary both temporally and spatially (Zhang et al. 2014). In actual canopies, the value of k calculated from Eq. 9.4 is sometimes greater than 1. In a canopy in which horizontal leaves are gathered at upper layers, light attenuates mainly by passing through only one thin layer with horizontally nonuniform distribution. For example, if k is estimated based on the irradiance/photon flux density measured just below one large leaf such as a lotus, it will be proportional to the negative logarithm of the transmittance of the leaf, being greater than 1 when the transmittance is less than $1/e$ (=0.37).

Note that the extinction coefficient k can be defined both in terms of total solar radiation (including all ranges of wavelength) and PAR (400–700 nm); the k value for solar radiation is likely to be smaller than that for PAR because of the higher absorbance and lower transmittance of leaves for PAR than for total solar radiation. In addition, k for artificial lighting may be different from that for solar radiation due to the differences in the light spectral distribution and the direction of incident light depending on the properties of the light source.
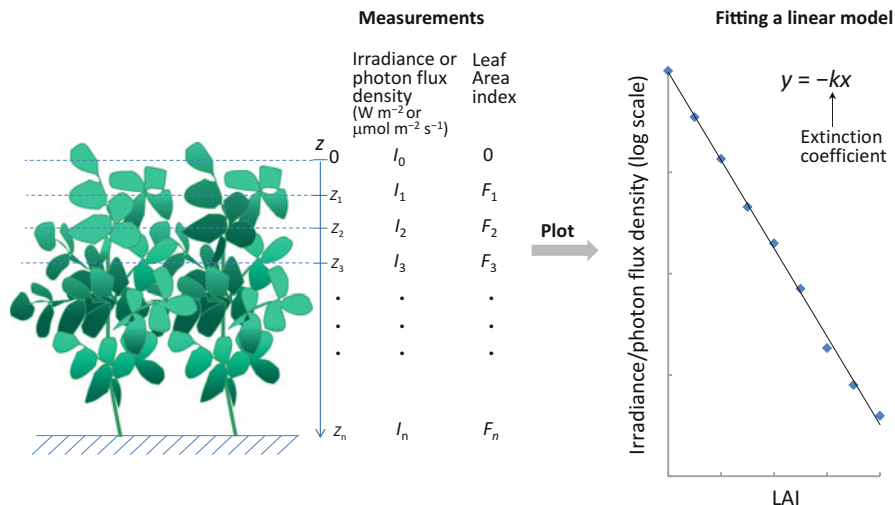
Fig. 9.3 Schematic diagram of estimation of extinction coefficient k based on the light distribution measurements within the canopy

9.4 Consideration of Spectral Properties Within the Canopy

As previously described, the light spectral distribution within the canopy is different from that outside the canopy, owing to light absorption and reflection by leaves. Normally, the proportion of green and/or far-red light is increased within the canopy (Kasperbauer 1971). Figure 9.4 shows examples of light spectra inside and outside the lettuce canopy under artificial lighting (with white LEDs). The spectral distribution of light within a canopy depends not only on the optical properties of the leaves but also on the spectral properties of lamps that are used for artificial lighting. In particular, for light from narrowband LED lamps, which contain no green and far-red light, light spectral distribution within a canopy greatly differs from those under sunlight. Green light may offer benefits for canopy photosynthesis, given that it can better penetrate the plant canopy and potentially increase plant growth by increasing photosynthesis from the leaves in the lower canopy (Kim et al. 2004). Far-red light may affect the morphogenesis of plants.

It should be noted that spectral properties of lamps also affect the extinction coefficient k and, thereby, the PPFD distribution within a canopy. Under light comprising only blue and red light, the extinction coefficient k is high and PPFD within a canopy is low.
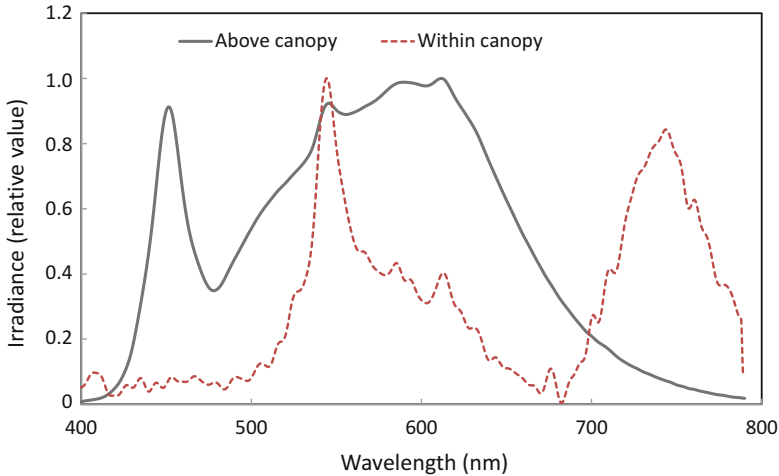
Fig. 9.4 Examples of light spectra measured above and within the lettuce canopy under white LED lighting

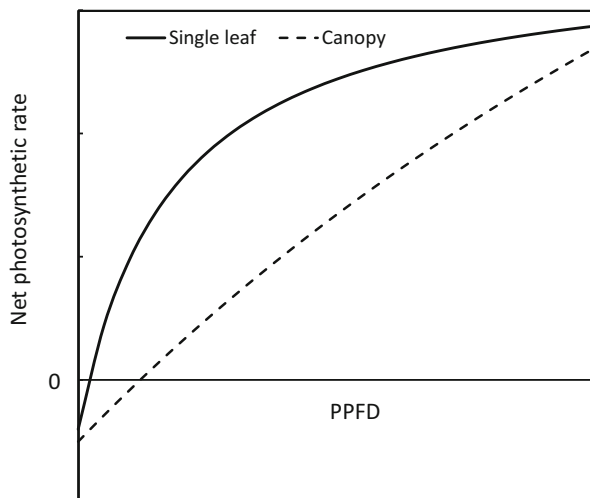## 9.5 Canopy Photosynthesis

9.5.1 Characteristics of Canopy Photosynthesis

A plant accumulates biomass through photosynthesis and normally has numerous leaves as organs for photosynthesis. In plant production, including plant factories, control of photosynthesis is critical for cultivation management, especially for cases in which there is vegetative growth. Although the photosynthetic properties of a single leaf is a baseline for considering the photosynthetic amount or rate of an individual plant or plant canopy, the photosynthetic properties of individual leaves vary over a plant or canopy depending on leaf age and position; for example, young leaves may be sink leaves with a low photosynthetic capacity. Furthermore, as described in the previous chapter, the spectral distribution of light will change when passing through a leaf.

Normally the light-photosynthetic curve of a canopy differs from that of a single leaf, showing higher or no light-saturated points in extreme cases (Fig. 9.5). This is caused by the existence of a PPFD distribution within the canopy. Increments of light irradiating a canopy can contribute to increasing the photosynthetic rates at the lower layers even if the PPFD at the top layer has reached the saturation point.

To estimate the photosynthetic rate of a canopy properly, the spatial distribution of environmental factors that affect photosynthesis, such as PPFD, CO_2 concentration, air temperature, humidity, and air current, should be identified.

Fig. 9.5 Typical patterns of light-photosynthetic *curves* of a single leaf and canopy. The *curves* were depicted using a rectangular hyperbolic function (Eq. 9.7) changing parameter values

9.5.2 Simple Method for Estimating Canopy Photosynthetic Rate

A basic method for estimating canopy photosynthesis is to sum up the photosynthetic rates of small parts of canopy that are assumed to be under uniform environmental conditions, in particular under uniform PPFDs. After the average PPFDs for these portions of canopy are estimated, their average photosynthetic rates are calculated. The photosynthetic rate of a single leaf depends on PPFD (see Chap. 8 for details), and the light-photosynthetic curve is not linear. Therefore, the average PPFDs are calculated for portions with similar PPFDs and used to estimate the average photosynthetic rate of these portions.

Monsi and Saeki (2005) proposed a simple estimation method for canopy photosynthetic rates using the extinction coefficient. The absorbed PPFD per unit leaf area at a given horizontal layer (in which LAI is dF) is expressed as $-dI/dF$; correspondingly, the PPFD on leaves at that layer is given by the following equation:

$$I' = -\frac{dI}{dF}\frac{1}{(1-\tau)} \, , \tag{9.5}$$

where τ is the leaf transmittance.

Because dI/dF can be calculated by differentiating I in Eq. 9.1 with respect to F, I' can be calculated using the following equation:

$$I' = I_0 k e^{-kF} \frac{1}{(1-\tau)} \ , \tag{9.6}$$

where I' represents the average PPFD on leaves at a given horizontal layer and can be used as an input to a model for the relationship between net photosynthetic rate and PPFD. Several functions have been proposed to express this relationship, with a common characteristic that they represent convex curves with saturated photosynthetic rates. Monsi and Saeki (2005) used a rectangular hyperbolic curve expressed by the following equations:

$$p = \frac{aI'}{(1+bI')} - r, \tag{9.7}$$

where a and b are constant and r is dark respiration. By inputting I' from Eq. 9.6 into this equation and integrating p with respect to F, canopy photosynthesis P can be expressed as:

$$P = \frac{a}{kb} \ln \frac{(1-\tau) + kbI_0}{(1-\tau) + kbI_0 e^{-kF}} - rF. \tag{9.8}$$

From this equation, we can estimate the optimal LAI that gives the maximum canopy photosynthesis (Hirose 2004).

In this calculation, photosynthetic properties of an individual leaf are assumed to be constant over the entire canopy; however, this will actually depend on the position within the canopy. For example, leaves at lower layers where PPFD is low may show the photosynthetic properties of shade leaves, i.e., high photosynthetic rates at low PPFD and low saturated rates. Models considering not only light distribution but also distribution of the leaf photosynthetic properties have also been proposed (e.g., Hirose and Werger 1987).

Note that simpler models can be adequate in several cases. Jones (1992) listed two limiting cases in which simpler models can be applied to estimate canopy photosynthesis:

(a) All leaves are at an acute angle to any direct radiation.

  – In this case, the total canopy photosynthesis is proportional to light interception with a proportionality constant ε_p. At high LAIs, where all radiation is intercepted, canopy photosynthesis is simply $\varepsilon_p I_0$.

(b) Very low LAI canopies.

  – In this case, single leaf photosynthetic models can be applied.

9.5.3 Growth Analysis

We can also estimate canopy photosynthesis using growth analysis, which evaluates how much biomass can be acquired by photosynthesis during a given period. The relative growth rate (RGR) defined as:

$$\text{RGR} = \frac{1}{W}\frac{\mathrm{d}W}{\mathrm{d}t} \ \left(\mathrm{d}^{-1}\right) \tag{9.9}$$

is commonly used for vegetative growth analysis, where W (g) is the dry weight of a plant and t is time (in days). In addition, the net assimilation rate (NAR) as growth rate per unit leaf area can be derived from the following equation and is related to the photosynthetic rate:

$$\text{NAR} = \frac{1}{L}\frac{\mathrm{d}W}{\mathrm{d}t} \ \left(\mathrm{g\ m^{-2}\ d^{-1}}\right), \tag{9.10}$$

where L is leaf area (m^2).

Under the assumption that RGR is constant during a given period, it can be calculated from the dry weights (W_1, W_2) and leaf areas (L_1, L_2) measured at different times (t_1, t_2) by the following equation:

$$\text{RGR} = \frac{\ln(W_2/W_1)}{t_2 - t_1}, \tag{9.11}$$

$$\text{NAR} = \frac{(W_2 - W_1)(\ln L_2 - \ln L_1)}{(L_2 - L_1)(t_2 - t_1)}, \tag{9.12}$$

RGR and NAR can be connected using the leaf area ratio (LAR):

$$\text{RGR} = \text{NAR} \ \times \text{LAR} \tag{9.13}$$

$$\text{LAR} = \frac{L}{W} \tag{9.14}$$

These calculations are based on invasive (destructive) measurement in which sampling is required for determining the dry weight or leaf area at different times. By contrast, relative leaf growth rate (RLGR) can be estimated nondestructively from images:

$$\text{RLGR} = \frac{\ln(L_2/L_1)}{t_2 - t_1} \tag{9.15}$$

For example, the RLGR of *Arabidopsis thaliana* was estimated automatically and used for phenotyping (Arvidsson et al. 2011). Normally, a projected area can be measured from an image. If a linear relationship is observed between the projected

area and the actual leaf area, RLGR can be estimated simply through image analysis (Ibaraki and Dutta Gupta 2014).

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