

## CHAPTER 11

# General principles of plant productivity

In a biological sense, plant production can be viewed as a system of conversion of solar energy into chemical energy that can be transported and stored. This conversion occurs through the reaction known as photosynthesis. The general principles underlying this process are fairly well understood. Since these principles are so important in managing production systems and exploiting their production potential, we will review them, in general, with an underlying emphasis on how plant management can lead to improved exploitation of photosynthesis. Readers are strongly advised to refer to basic text books on plant physiology, several of which are available, for a thorough understanding or recapitulation of the subject.

### 11.1. Photosynthesis

Photosynthesis consists essentially of carbon "fixation" in the green tissues of plants, in the presence of sunlight. The overall reaction can be written as:



The photosynthetic apparatus of the plant is the chloroplast, which is a lens-shaped organ with a 1-10 *um* width. It has two parts: the lamellae (membranes), which are concentrated areas of photosynthetic pigments, and the stroma, which mainly contains fluids and is less dense. Photosynthesis consists of two reactions, the so-called light reaction (photophosphorylation) and the dark reaction (CO<sub>2</sub> fixation) (Figure 11.1). The light reaction occurs in lamellae and consists of the oxidation of water and production of chemical energy in the form of reduced nicotinamide adenine dinucleotide phosphate (NADPH), and the phosphorylation of adenosine diphosphate (ADP) to adenosine triphosphate (ATP). ATP is synonymous with energy in biological systems. Both NADPH and ATP are needed for the conversion of carbon dioxide to stable organic molecules, the process that occurs during the dark reaction.

The radiant energy available for photosynthesis comes from the sun. The solar radiation that is received at the earth's surface, when that surface is

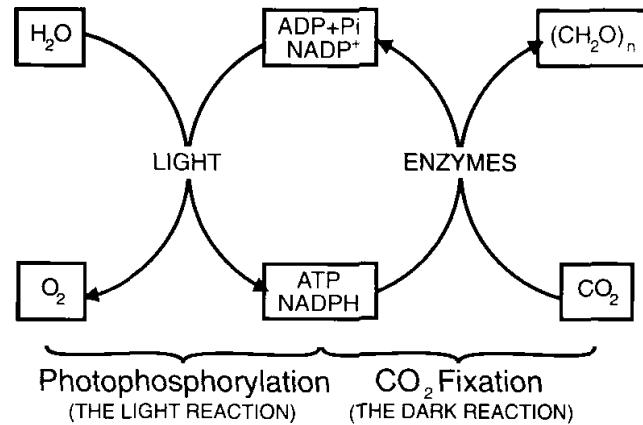


Figure 11.1. The light and dark reactions that make up photosynthesis. The energy flows from light (irradiance) to high-energy intermediate compounds (ATP and NADPH) and then to long-term energy in bonds connecting carbon atoms of organic molecules.

Source: Gardner *et al.* (1985).

perpendicular to the sun's rays, ranges from 14 to 1.7 cal cm<sup>2</sup> min<sup>-1</sup> on a clear day. The visible spectrum of solar radiation (400 to 700 nm wavelengths) corresponds to 44-50% of the total solar radiation entering the earth's atmosphere. This visible spectrum, which plants use for photosynthesis, is called the *photosynthetically active radiation* (PAR). According to the quantum theory, light travels in a stream of particles called *photons*, and the energy present in one photon is called a *quantum*. Since PAR measurements are usually based on photon flux density within the 400-700 nm wavelengths, they are also called *photosynthetic photon flux density* (PPFD). Its unit of measurement is the Einstein (E) which is defined as one mole of photons; thus, PAR is often listed as  $\mu\text{E}$  (or,  $\mu\text{ mol}$ ) m<sup>-2</sup> s<sup>-1</sup>.

Before the 1960s, it was believed that the reduction of CO<sub>2</sub> only proceeded according to a pattern or pathway known as the Calvin Cycle (after M. Calvin). In this process, CO<sub>2</sub> combines with the pentose sugar ribulose diphosphate to produce two molecules of 3-phosphoglyceric acid (3-PGA) and finally hexose. Since the first product that can be measured after adding radioactive CO<sub>2</sub> (<sup>14</sup>CO<sub>2</sub>) is a three-C molecule (3-PGA), this pathway is known as the C<sub>3</sub> pathway, and species that fix carbon through this pathway are known as C<sub>3</sub> plants.

In the 1960s Hatch and Slack presented convincing evidence that another pathway for CO<sub>2</sub> fixation existed in some species. Here, CO<sub>2</sub> combines with phosphoenolpyruvate (PEP) to produce four-carbon compounds (oxaloacetate, malate, and aspartate), which are then translocated to vascular sheath cells where they are converted to pyruvate. Since the first detectable product of photosynthesis in this pathway is a 4-C molecule, the pathway is known as the C<sub>4</sub> pathway, and species with this pathway are known as C<sub>4</sub> plants.

A third mechanism, known as the Crassulacean Acid Metabolism (CAM) has also been found to occur in a number of species (e.g., pineapple). Here, the

uptake of carbon dioxide occurs mainly in the dark when their stomata remain open; the organic acids that are accumulated are then transformed to carbohydrates and other products during the day when the light reaction provides the necessary energy. There is little uptake of CO<sub>2</sub> during the day because of stomatal closure. However, under favorable moisture conditions, many CAM species change stomatal functions and follow a carboxylation pathway similar to that of C<sub>3</sub> species.

The C<sub>3</sub> and C<sub>4</sub> pathways are the two major photosynthetic pathways. C<sub>3</sub> species include many grasses such as wheat, oats, barley, rice, rye, and dicot species such as legumes, cotton, tobacco, and potatoes, and almost all trees. C<sub>4</sub> species include warm-season grasses such as maize, sorghum, and sugarcane. The CAM plants are mostly succulent species adapted to arid conditions where low transpiration is an adaptive mechanism. Only a few agriculturally important plants have been classified as CAM species; these include pineapple and *Agave* spp.

Table 11.1. Essential characteristics and comparison of plants with C<sub>3</sub>, and C<sub>4</sub>, and CAM pathways of photosynthesis.

	C <sub>3</sub>	C <sub>4</sub>	CAM
	cool season grass (wheat, oats, rye) dicots: legumes, tobacco, potato	warm season grasses (maize, sugarcane) dicots: no major crops, but some weeds	About 10 families (e.g.: pineapple, agave, opuntia)
Taxon. diversity	Very wide	Many grasses No/very few trees	Very few species
Anatomy			
Chloroplast	<i>Not</i> in vase. sheath	Present in vase, sheath	
CO <sub>2</sub> fixed: (enzyme)	RuBP carboxylase	PEP carboxylase	in night; energy from glycolysis
Habitat	no pattern	open, warm, saline	open, warm, saline
Photorespiration	high	low	low
Light sat. point (lux)	65000	> 80000	like C <sub>3</sub>
Max P.S. (mg dm <sup>-2</sup> h <sup>1</sup> )	30	60	3
Max. growth rate (g dm <sup>2</sup> d <sup>1</sup> )	1	4	0.02
WUE* (g H <sub>2</sub> O gCO <sub>2</sub> <sup>-1</sup> )	600	300	50
CO <sub>2</sub> comp. point (ppm)	50	5	2 (in dark)
Stomates:			
day	open	open	closed
night	closed	closed	open

\* Water use efficiency.

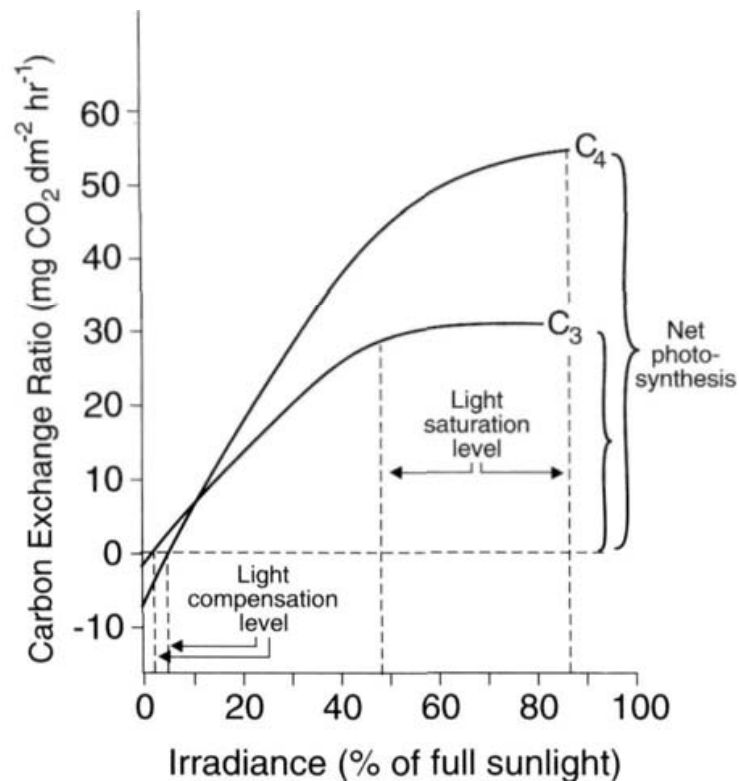


Figure 11.2. General patterns of light-response curves for C<sub>3</sub> and C<sub>4</sub> plants. The light compensation level is the irradiance level at which CO<sub>2</sub> uptake due to photosynthesis is equal to CO<sub>2</sub> evolution due to respiration. The light saturation level is an irradiance level at which an irradiance increase would not result in a significant increase in carbon exchange rate (CER).

Source: Adapted from Gardner *et al.* (1985).

Table 11.1 gives a comparison among C<sub>3</sub>, C<sub>4</sub>, and CAM plants. One of the main differences between the C<sub>3</sub> and C<sub>4</sub> plants is the increased photosynthetic efficiency of the latter. This is because these (C<sub>4</sub>) species have little or no photorespiration (respiration in light); on the other hand, C<sub>3</sub> species do have photorespiration, which results in CO<sub>2</sub> evolution (loss) in light in these species (see section 11.2 for an explanation of respiration).

In general, when the amount of available light (PAR) increases, photosynthesis increases up to a certain level. Light compensation level is the light level at which CO<sub>2</sub> uptake equals CO<sub>2</sub> evolution from respiration; in other words, when the carbon exchange rate (CER) equals zero. If the light level continues to increase, CER increases until a point called the light saturation level, after which an increase in light level does not result in a proportionate increase in CER (Figure 11.2). The light saturation levels for most C<sub>4</sub> plants are comparatively higher than for C<sub>3</sub> plants; this means CO<sub>2</sub> uptake by C<sub>4</sub> plants continues to increase at light levels higher (or those closer to full sunlight) than those for C<sub>3</sub> species. Additionally, C<sub>4</sub> species use dimmer light better than C<sub>3</sub> plants do. However, the efficiency of CO<sub>2</sub> uptake at low irradiance levels generally is higher for C<sub>3</sub> plants than for C<sub>4</sub> plants, because the energy requirement for CO<sub>2</sub> reduction is higher in C<sub>4</sub> plants.

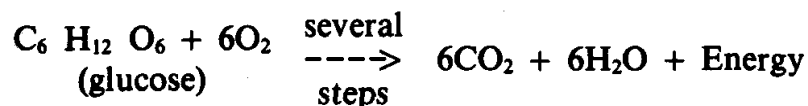
As temperature increases, the loss of carbon by photorespiration becomes more important than the lower energetic requirements of CO<sub>2</sub> reduction in C<sub>3</sub> plants, and the quantum yield (moles of CO<sub>2</sub> taken up per Einstein absorbed) decreases to values below those of C<sub>4</sub> plants. Thus, the effectiveness of generally higher photosynthetic capacities in C<sub>4</sub> plants is realized mainly under optimal growth conditions in an open canopy (Tieszen, 1983).

## 11.2. Plant productivity

Plant productivity, i.e., the amount of growth that can be attained by a plant within a given period of time, is a function of the net rate of photosynthesis (P<sub>N</sub>), which is the difference between gross photosynthesis (P<sub>G</sub>) and respiration (R):

$$P_N = P_G - R.$$

Respiration involves the oxidation (or breakdown) of complex substances such as sugars and fats. The general reaction is:



Photosynthesis and respiration are, in many ways, similar but opposing reactions. Respiration uses energy from photosynthesis. Photosynthesis results in increased dry weight due to CO<sub>2</sub> uptake, while respiration results in the release of CO<sub>2</sub>, and therefore reduction of dry weight (Table 11.2). Both processes are essential. The simple carbohydrates formed by photosynthesis are transformed by respiration to the structural, storage, and metabolic substances required for plant growth and development. Under optimal conditions, respiration accounts for about a 33% loss or reduction of photosynthates.

In crop physiology, the concept of *Leaf Area Index* (LAI) is widely used in growth analysis. LAI is the ratio of the leaf area (one side only) of the plant to the ground area. Productivity of crop canopies is usually expressed by the term *Crop Growth Rate* (CGR), which is dry matter accumulation per unit of land

**Table 11.2. Simple comparison between photosynthesis and respiration.**

### PHOTOSYNTHESIS

1. Only in green cells
2. Only in light
3. Uses H<sub>2</sub>O and CO<sub>2</sub>
4. Releases O<sub>2</sub>
5. Solar energy is converted into chemical energy; used to produce carbohydrates
6. Causes increase in weight

### RESPIRATION

1. In all active living cells
2. At all times
3. Uses products of photosynthesis
4. Releases H<sub>2</sub>O and CO<sub>2</sub>
5. Energy is released by the breakdown of carbohydrates and proteins
6. Causes decrease in weight

area per unit of time. It is usually expressed as  $\text{g nr}^2 (\text{land area}) \text{ day}^{-1}$ . Since leaf surfaces are the primary photosynthetic organs, crop growth is also sometimes expressed as *net assimilation rate* (NAR), which is the dry matter accumulation per unit of leaf area per unit of time, usually expressed as  $\text{g m}^{-2} (\text{leaf area}) \text{ day}^{-1}$ . The NAR is a measure of the average net  $\text{CO}_2$  exchange rate per unit of leaf area in the plant canopy; therefore  $\text{NAR} \times \text{LAI} = \text{CGR}$ .

Various calculations, estimates, and projections of plant productivity have been made for a number of settings. Loomis and Williams (1963) gave a thoughtful analysis of the hypothetical maximum dry matter production rate. Based on various assumptions, they estimated that the maximum CGR (or, potential productivity) during the 100-day period from June 1st to September 8th in a location in the United States was  $77 \text{ g nr}^2 \text{ day}^{-1}$ , amounting to  $770 \text{ kg ha}^{-1} \text{ day}^{-1}$ , or  $281 \text{ t dry matter ha}^{-1} \text{ yr}^{-1}$ . Actual measurement of short-term CGR recorded for several crop species under ideal conditions came within 17-54% of this figure (Gardner *et al.*, 1985).

In agriculturally advanced areas, photosynthetic efficiencies (meaning the efficiency of converting solar energy into photosynthates, in terms of equivalent energy units) of only 2-2.5% are obtained. On a global basis, efficiencies of less than 1% are very common (San Pietro, 1967). For high-intensity, multiple cropping systems involving three crops per year and total crop duration of up to 340 days per year, Nair *et al.* (1973) reported photosynthetic efficiencies ranging from 1.7% to 2.38% in northern India (29°N, 79°E, and 240 m altitude). Extremely high short-term productivities have been reported from some natural grassland ecosystems. For example, above-ground net primary productivity (ANPP) as high as  $40 \text{ g nr}^2 \text{ day}^{-1}$  ( $= 1461 \text{ ha}^{-1} \text{ yr}^{-1}$ ), with values consistently  $> 20 \text{ g nr}^2 \text{ day}^{-1}$ , have been recorded during the wet season from the Serengeti ecosystem of Tanzania; these are higher than for any other managed or natural grasslands in the world (Sinclair and Norton-Griffiths, 1979). In forestry systems, mean net primary productivity values of 10-35 and 10-25  $\text{t ha}^{-1} \text{ yr}^{-1}$  have been reported for tropical rain forest and tropical seasonal forest, respectively (Jordan, 1985). These values, however, are influenced by a number of factors such as sampling error, choice of sites, and species composition of the system; therefore, great caution should be exercised in using these values of productivity as feasible goals. Nevertheless, they give some indication of the potential that could be achieved. Field measurements of such photosynthetic efficiency or productivity figures are not yet available for agroforestry systems. Young's (1989) calculations, presented in Chapter 16, give 201 dry matter per hectare per year as a conservative estimate of productivity in humid lowland agroforestry systems. Considering that roots constitute roughly 33% of total photosynthate, 201  $\text{ha}^{-1} \text{ yr}^{-1}$  of above-ground dry matter would represent 301  $\text{ha}^{-1} \text{ yr}^{-1}$  of total dry matter production, a figure comparable to those of most high-input agricultural systems. It seems reasonable to surmise that the productivity of agroforestry systems is comparable to, if not better than, that of high-input agricultural systems.

However, such comparisons of total productivity have some limitations. In practical terms, it is the economically useful fraction of total productivity that is more meaningful than total productivity *per se*. *Harvest Index* is a term that has been used to denote this fraction:

$$\text{Harvest Index} = \frac{\text{Economic Productivity}}{\text{Biological Productivity}}$$

A discussion on the usefulness of harvest index and other measures of productivity of mixtures is included in Chapter 24 (section 24.1).

### 11.3. Manipulation of photosynthesis in agroforestry

Selection of species to be used in agroforestry must be based on cultural and economic as well as environmental factors. However, some general principles related to photosynthetic pathways will be useful when choosing species for agroforestry systems. For example, under sound agronomic management in the tropics and subtropics, C<sub>4</sub> monoculture systems should be more productive than C<sub>3</sub> monoculture systems (Monteith, 1978). This may be significant in agroforestry systems where annual or seasonal canopy types (as in hedgerow intercropping) can be found as well as the permanent overstory type. In the annual or seasonal type, it is imperative to build up leaf area as quickly as possible; C<sub>4</sub> plants are the best candidates for this function. In conditions with a permanent woody overstory, the options are limited. Most trees possess the C<sub>3</sub> pathway; thus, the overstory will be C<sub>3</sub>. If shading is significant, the understory preference should be for C<sub>3</sub> plants as they have a greater efficiency of CO<sub>2</sub> uptake at lower irradiance levels than C<sub>4</sub> plants. If, however, the overstory is open, C<sub>4</sub> types could be used as understory species (Tieszen, 1983). Photosynthetic pathways of different species will undoubtedly be an important physiological consideration in the search for "new" species and screening of local species for their agroforestry potential.

Another factor that affects photosynthetic rates is the CO<sub>2</sub> concentration in the atmosphere. Atmospheric concentration of CO<sub>2</sub> has increased from about 300 ppm (0.03%) in the 1960s to about 340 ppm in the late 1980s, caused mainly by burning of fossil fuels and, to some extent, burning of forests and other biomass (Crutzen and Andreae, 1990). In general, when the CO<sub>2</sub> concentration increases, the photosynthetic rate is also expected to increase. However, the major environmental concern that presently prevails with regard to the adverse effect of an increase in atmospheric CO<sub>2</sub> concentration is the possible increase in global temperature (through absorption of infrared bands of light) and its influence on global weather patterns. Changing climates promise to have a great effect on plant productivity. In a practical sense, CO<sub>2</sub> levels in the atmosphere are not expected to fluctuate to the extent that they will have a major influence on the productivity of agroforestry systems.

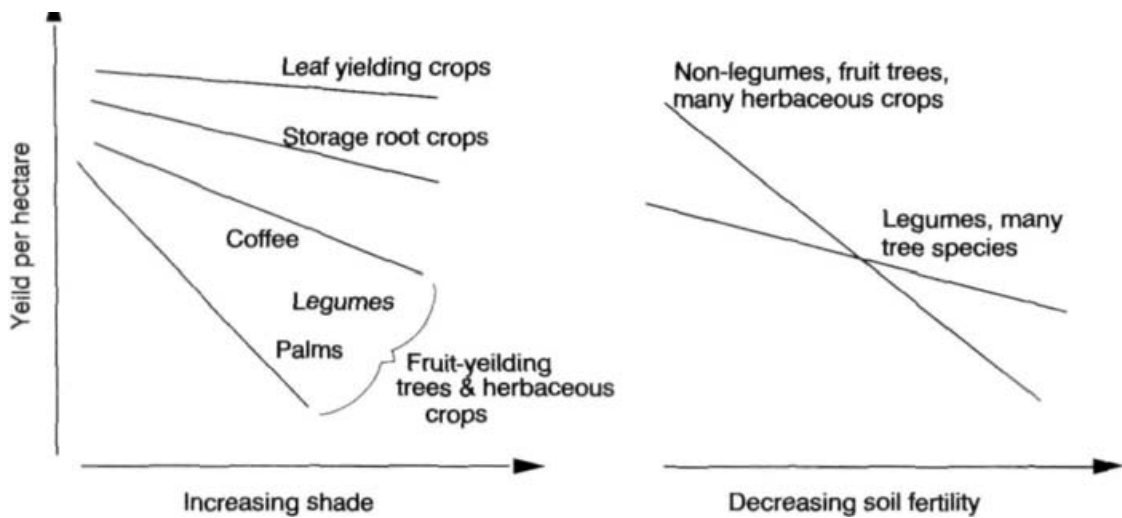


Figure 11.3. Diagrammatic representation of general crop differences in response to shading and soil fertility (Also see Figure 13.3).

Source: Cannell (1983).

The other major factors that affect photosynthetic rates are temperature and the availability of moisture and nutrients. Although agroforestry combinations can cause considerable modifications in the availability of these growth factors (see Chapter 13), under practical (field) conditions, such fluctuations may not be marked enough to cause significant effects on photosynthetic rates. However, various plants react differently in their response to the interacting effects of shade and nutrients, and possibly of shade and temperature. A diagrammatic representation of the general response of some common groups of crops to shading and soil fertility, as suggested by Cannell (1983), is given in Figure 11.3. Screening crop varieties for their specific responses, and understanding the mechanisms of the responses and manipulating them through easy-to-adopt management practices will be challenging areas for future research in agroforestry.

The major management options for manipulating photosynthesis of plant communities in agroforestry systems, at present, are based on the manipulation of the light (radiation) profile. In order for a plant community to use solar radiation effectively, most of the radiation must be absorbed by green, photosynthetic tissues. While the selection of species and their arrangement and management determine the photosynthetic efficiency of the whole plant-community, the angle, disposition, number, size, and arrangement of leaves are important factors that determine the photosynthetic area and capacity of individual plants. Multispecies plant communities, e.g., homegardens, obviously have multiple strata of leaf canopies, and, hence, a much higher LAI than in monospecific stands, which often translates to higher photosynthetic rates. However, higher LAI need not necessarily lead to proportionately higher photosynthetic rates. One of the major considerations in the development of high-yielding varieties of cereals such as rice and wheat that led to the so-called



green revolution was the development of varieties that possessed a canopy with an optimum LAI with little or reduced shading of lower leaves by the upper leaves.

Solar-energy interception by different components of a multi-layered canopy with large vertical gaps between the constituent canopy units, and the distribution of **PAR** within these units, are important factors that determine the productivity of mixtures. In continuous-canopy crops such as cereals, light interception and distribution are governed by the Beer-Lambert law:

$$I_i/I_0 = e^{-kL}$$

where  $I_j$  = PAR below the  $i^{\text{th}}$  layer of leaves

$I_0$  = **PAR** above the canopy

$e$  = natural log (2.71828)

$k$  = a constant (called the extinction coefficient) depending, to some extent, on LAI and leaf characteristics

$L$  = LAI.

In practical terms, the equation means that the amount of radiation (PAR) that is transmitted through a canopy is dependent upon the incident radiation and leaf characteristics. Various modifications of this basic equation have been suggested to describe light transmission patterns in discontinuous canopies such as agroforestry mixtures (e.g., Jackson, 1983; Jackson and Palmer, 1979; 1981).

With respect to productivity considerations of agroforestry systems, it should be possible to estimate the **PAR** intercepted by each component of the systems at any given time, and to integrate this estimate to reflect the time they occupy the space. Theoretically, the productivity of plants intercropped under a tree stand will be negligible if the tree canopy is able to intercept most of the available light. However, many tree crops are inefficient in the interception of radiant energy because they take many years to produce a full canopy. Furthermore, the full canopy may still be inefficient (due to biological or management reasons) in light interception at given times during the year. This is the rationale and cause for many intercropping successes in plantation-crop combinations with plants such as coconut (Nair, 1979; **1983**; see Chapter 8). It may well be that the biological efficiency of multistory agroforestry systems will be greater by having trees with small, erect leaves (with low  $k$  values) as the upper story, and plants with large horizontal leaves (with high  $k$  values) at the ground level. Caution is needed here, however; as Jackson (1983) points out, generalizations by analogy may often be misleading.

It is, therefore, clear that understanding the way in which the components of a mixed plant community share solar radiation is a critical factor in the assessment and management of the productivity of agroforestry systems. The curve of net photosynthesis saturates and levels off at about 25% full sunlight for most  $C_3$  plants (Figure 11.2); consequently, any leaf receiving more than this level of radiation may not be making the full use of it. We could thus have

a multistory plant configuration with leaves at the top receiving full sunlight, and other leaf strata, at various distances below, receiving less than full sunlight, but still operating at or near the peak photosynthetic rate.

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