Tansley Review No. 32 Achievable Productivities of Certain CAM Plants: Basis for High Values Compared with C_3 and C_4 Plants

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CONTENTS

SUMMARY

CAM species, which taxonomically are at least five times more numerous than C_4 species, often grow slowly, as is the case for various short-statured cacti and many epiphytes in several families. However, slow growth is not a necessary corollary of the CAM photosynthetic pathway, as can be appreciated by considering the energetics of CO_2 fixation. For every CO_2 fixed photosynthetically, C_3 plants require 3 ATP and 2 NADPH, whereas the extra enzymatic reactions and compartmentation complexity for C_4 plants require 4 or 5 ATP and 2 NADPH, and CAM plants require 5·5–6·5 ATP and 2 NADPH. Photorespiration in C_3 plants can release some of the CO_2 fixed and also has an energetic cost, whereas photorespiration is much less in C_4 and CAM plants. Therefore, CAM plants can perform net CO_2 fixation 15 % more efficiently than C_3 plants, although 10 % less efficiently than C_4 plants.

Using a simple model that assumes 8 photons per CO_2 fixed and a processing time per excitation of 5 ms, a maximum instantaneous rate for net CO_2 uptake of 55 μmol m^{-2} s^{-1} is predicted. Measured maximal rates average 48 μmol m^{-2} s^{-1} for leaves of six C_3 species with the highest rates and 64 μmol m^{-2} s^{-1} for six such C_4 species; CAM plants take up CO_2 mainly at night, which is not directly related to the instantaneous rate of photon absorption. Net CO_2 uptake integrated over 24 h, which is more pertinent to productivity than are instantaneous CO_2 uptake rates, is similar for the three pathways, although the higher water-use efficiency of CAM plants can be an advantage during drought.

Abbreviations: CAM, Crassulacean acid metabolism; EPI, environmental productivity index; LAI, leaf area index; PEP, phosphoenolpyruvate; PPFD, photosynthetic photon flux density; SAI, stem area index; WUE, water-use efficiency.

Canopy architecture is crucial for the distribution of the photosynthetic photon flux density (PPFD) over the shoot, which determines net CO_2 uptake per unit ground area and hence determines productivity. Maximal productivity for idealized canopies under optimal conditions is predicted to be about 100 Mg d. wt $ha^{-1} yr^{-1}$ (1 Mg = 1 tonne), whereas actual values of environmental factors in the field approximately halve this prediction. The influence of environmental factors on net CO_2 uptake can be quantified using an environmental productivity index (EPI), which predicts the fractional limitation on net CO_2 uptake and is the product of a water index, a temperature index, and a PPFD index (nutrient effects can also be included).

Using EPI with a ray-tracing technique to determine the PPFD index and taking into account respiration and carbon incorporated structurally, maximal productivity of CAM plants is predicted to occur at leaf or stem area indices of 4–5. In experiments designed using such shoot area indices, annual above-ground dry-weight productivities averaging 43 Mg $ha^{-1} yr^{-1}$ have recently been observed for certain agaves and platyopuntias. In comparison, the measured average annual productivity of the most productive plants is 49 Mg $ha^{-1} yr^{-1}$ for six agronomic C_4 species, 35 Mg $ha^{-1} yr^{-1}$ for six agronomic C_3 species, and 39 Mg $ha^{-1} yr^{-1}$ for six C_3 tree species. Thus, CAM plants are capable of similar high productivities, which can become especially advantageous in regions of substantial water stress. Recognition of the high potential productivity of certain CAM species under optimal environmental conditions, exceeding that of most C_3 species, may increase the cultivation of such CAM plants in various areas in the future.

I. INTRODUCTION

What limits the biomass productivity of plants? What are the highest values achievable? Here an attempt will be made to address such questions, beginning with a cellular and energetic consideration of the three pathways for CO_2 fixation – C_3, C_4, and CAM. A thesis to be developed is that some CAM plants can achieve high productivities. Indeed, their productivities in certain habitats and under certain agronomic conditions can exceed the productivities of most C_3 and C_4 plants (Nobel, 1988). This contradicts the conventional view that CAM plants, such as cacti, grow relatively slowly (Black, 1973; Winter, 1985). For instance, the widely distributed cactus *Coryphantha vivipara*, which occurs from northern Mexico through the western United States to southern Canada, attains a height of only 8 cm after 50 or more years of growth (Nobel, 1981; Benson, 1982). Certain dwarf cacti have an even slower growth rate than *C. vivipara*, such as *Ariocarpus fissuratus*, *Epithelantha bokei*, and *Mammillaria lasiacantha*, sympatric species occurring in the Chihuahuan Desert than extend less than 2 cm above the ground at maturity (Glass & Foster, 1974; Nobel *et al.*, 1986). Are such low growth rates peculiar to these species and their habitats, or a consequential limitation of the biochemical pathway and cellular characteristics involved with CAM?

Of the approximately 250000 species of higher vascular plants, CAM is exhibited by 15000–20000 species in over 30 families, making it more than five times more common than is the C_4 pathway on a species basis (Winter *et al.*, 1983; Ting, 1985; Winter, 1985; Lüttge, 1987; Salisbury & Ross, 1991). In particular, CAM evidently occurs in at least 5000 species in the Orchidaceae (20000 species in the family) and about 500 species in both the Asclepiadaceae (2500 species) and the Euphorbiaceae (7000 species; Thorne, 1983; Winter *et al.*, 1983). CAM is presumed to be the prevalent pathway in the Aizoaceae (2100 species in family), Bromeliaceae (2000 species), Cactaceae (1600 species), and Crassulaceae (1500 species; Smith, 1984; Gibson & Nobel, 1986).

The common assumption about the frequency of the various pathways among plants is probably based on agronomic species. Of the 150 most intensively cultivated, edible horticultural crops, about 10 use the C_4 pathway and only two use the CAM pathway (*Ananas comosus* and *Opuntia* spp.; Hackett & Carolane, 1982; Jones, 1985; Simpson & Conner-Ogorzaly, 1986). Also, 8 out of the world's 10 most agriculturally damaging weeds use the C_4 pathway (Holm *et al.*, 1977), again

suggesting that C_4 species are more common than CAM species. However, CAM species are extensively utilized in certain developing countries, for which agronomic information is not as widely available. For instance, the fruit of over 20 species of cacti are harvested for human consumption in Latin America (Benson, 1982; Felger & Moser, 1985; Russell & Felker, 1987) and 10 species of agaves are used to produce alcoholic beverages in Mexico alone (Gentry, 1982; Tello-Balderas & García-Moya, 1985; Valenzuela, 1985; Nobel, 1990).

To provide a background for evaluating the maximal productivity of CAM plants, first the cellular compartmentation, biochemistry, and energetics of CO_2 fixation in CAM are considered and compared with these processes in C_3 and C_4 plants. This leads to a consideration of net CO_2 uptake per unit surface area for these three main biochemical pathways. Because such CO_2 uptake is highly influenced by the location of the shoot surfaces in the canopy, canopy architecture in general and an environmental productivity index (EPI) in particular are also discussed. Maximal biomass productivities are then considered for all three pathways, highlighting the productivities for certain CAM plants under optimal conditions. The high productivities for these CAM species not only has a logical cellular basis but also has many implications for future cultivation of CAM plants in specific regions.

II. BIOCHEMISTRY OF C_3, C_4 AND CAM PLANTS

1. *Cellular compartmentation*

The key differences among the three photosynthetic pathways are the site for the initial CO_2 incorporation into an organic molecule as well as the timing, location, and biochemical pathway for the processing of such fixed CO_2 (Cockburn, 1985; Gregory, 1989). In C_3 plants, the process is the simplest: CO_2 is incorporated into a 5-carbon compound in the mesophyll cell chloroplasts, leading to the formation of two 3-carbon molecules in the chloroplasts (Fig. 1 *a*).

For C_4 plants, the overall CO_2 fixation process is more complex. CO_2 is initially incorporated into a 4-carbon molecule in the cytosol of mesophyll cells; this molecule is enzymatically transformed and shuttled to the bundle sheath cells surrounding the vascular bundles, where it is decarboxylated (Fig. 1 *b*). This leads to locally high concentrations of CO_2, which is processed in the chloroplasts of the bundle sheath cells in the same manner as CO_2 is processed by C_3 plants.

In contrast to the situation for C_3 and C_4 plants, stomatal opening and net CO_2 uptake occur predominantly at night for CAM plants. The CO_2 entering at night is incorporated into a 4-carbon compound in the cytosol of mesophyll cells (of leaves) and is then transported into their vacuoles for overnight storage (Fig. 1 *c*); when stem succulents are also considered, the more general expression, chlorenchyma cells, replaces the expression mesophyll cells. During the following daytime, the 4-carbon compound diffuses out of the vacuoles and is decarboxylated in the cytosol or in the mitochondria. The released CO_2 is fixed as for C_3 plants in the chloroplasts of chlorenchyma cells. Because the stomata of CAM plants tend to remain closed during the daytime, the CO_2 concentration in the chlorenchyma can then become quite high, especially in the late morning.

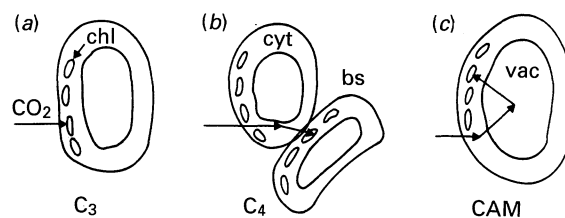**Figure 1.** Compartmentation of the three main photosynthetic pathways. The C_3 pathway (*a*) involves only the chloroplasts in mesophyll cells, the C_4 pathway (*b*) involves various compartments in mesophyll and bundle sheath cells, and the CAM pathway (*c*) involves three compartments in one cell in the chlorenchyma. Abbreviations: bs, bundle sheath cell; chl, chloroplast; cyt, cytosol; vac, vacuole.

2. *Biochemical pathways*

The cellular compartmentation (Fig. 1) underlies the relative complexity of the three photosynthetic pathways (Edwards & Walker, 1983; Salisbury & Ross, 1991; Taiz & Zeiger, 1991). For C_3 plants during the daytime, CO_2 diffuses from the atmosphere through the stomatal pores and eventually to the chloroplast stroma, where ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) catalyses the incorporation of CO_2 into ribulose-1,5-bisphosphate, yielding two molecules of 3-phosphoglycerate. The photosynthetic carbon reduction cycle in the chloroplast stroma then leads to the regeneration of ribulose-1,5-bisphosphate as well as a net production of glucose, which is often incorporated into starch (upper left of Fig. 2).

For C_4 plants during the daytime, CO_2 diffuses from the atmosphere through the stomatal pores to the cytosol of mesophyll cells, where phosphoenolpyruvate (PEP) carboxylase catalyses the incorporation of CO_2 (in the form of bicarbonate) into PEP, yielding the dicarboxylic acid oxaloacetate. Oxaloacetate can be reduced to malate by the addition of two hydrogens using NADPH (catalysed by malate dehydrogenase), a reaction that occurs in the chloroplasts. Also, a 4-carbon dicarboxylic aminated acid, aspartate, can be formed in the cytosol via transamination of oxaloacetate by alanine with the formation of pyruvate as a product. Malate then diffuses (probably through plasmodesmata) into bundle sheath cells (Fig. 1 *b*), where decarboxylation to pyruvate and CO_2 can occur with the regeneration of NADPH (catalysed by NADP malic enzyme). Also, aspartate diffuses into the bundle sheath cells of C_4 plants, where it is transaminated back to oxaloacetate and then reduced (via a NAD-dependent malate dehydrogenase) to malate, which is decarboxylated (via a NAD malic enzyme), meanwhile leading to the regeneration of alanine. In some species, oxaloacetate formed from aspartate is decarboxylated (via PEP carboxykinase) in an ATP-requiring reaction leading to PEP. The CO_2 released from oxaloacetate or malate diffuses into the chloroplasts and is fixed by Rubisco, as for C_3 plants.

Similar to the case for C_4 plants, CAM plants also use PEP carboxylase in the cytosol of chlorenchyma cells for the initial fixation of CO_2, but the fixation occurs at night (Fig. 2). Cytosolic
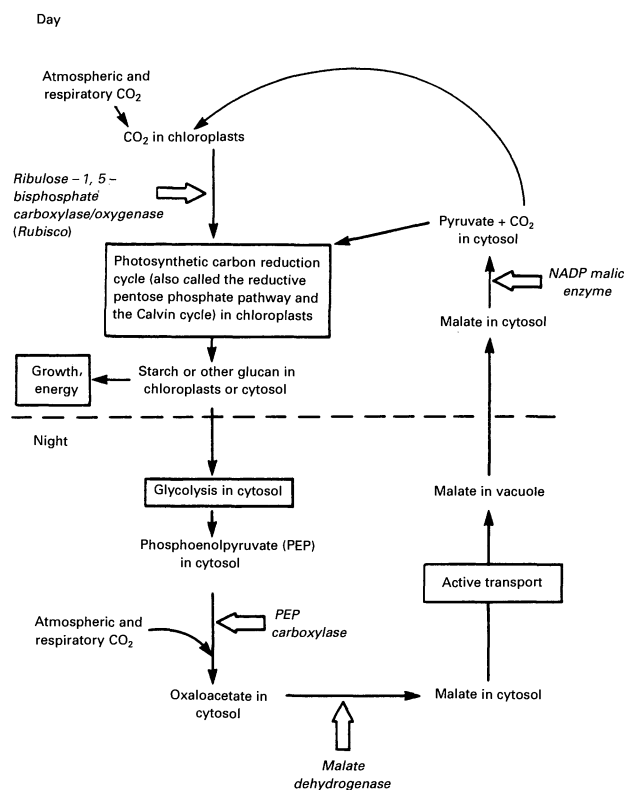

Figure 2. Summary of key biochemical events and pathways occurring in many CAM plants. Cycles or processes are indicated in boxes and enzymes in italics. Used by permission from Nobel (1988) (© Cambridge University Press).

malate dehydrogenase then leads to the formation of malate, which is actively transported into the vacuole of that chlorenchyma cell for overnight storage (Fig. 1c). Malate that diffuses from the vacuole during the following daytime is decarboxylated in the cytosol or in the mitochondria, yielding CO_2 that then diffuses into the chloroplasts, where it is refixed by Rubisco using the same photosynthetic carbon reduction cycle as in C_3 plants (Fig. 2). Another dicarboxylic organic acid that increases nocturnally in some CAM plants is citrate, and aspartate as well as oxaloacetate can be involved in the daytime decarboxylation reactions. Most CAM plants can perform C_3 photosynthesis during the daytime using CO_2 directly from the atmosphere (Fig. 2), whereas C_3 and C_4 plants do not perform CAM during the night-time, an important distinction among the pathways.

3. Comparative energetics

All three photosynthetic pathways involve the photosynthetic carbon reduction cycle, for which 3 molecules of ATP and 2 molecules of NADPH are required per molecule of CO_2 fixed (Edwards & Walker, 1983; Nobel, 1991; Salisbury & Ross, 1991; Taiz & Zeiger, 1991). In addition, the C_4 and CAM pathways have energy requirements for the enzymatic steps besides those in common with the C_3 pathway.

The reaction converting oxaloacetate to malate requires 1 NADPH, which is regenerated when malate is decarboxylated in both C_4 and CAM plants. Also, in C_4 and CAM plants that form aspartate as part of the photosynthetic process, no net pyridine nucleotide consumption or production is involved in the organic acid part of the cycle. To regenerate PEP from pyruvate, or for the net reaction of alanine plus CO_2 to form aspartate, 2 ATP are required. For those C_4 plants decarboxylating oxaloacetate directly to PEP, only 1 ATP is needed for the organic acid part of the pathway. The three different carboxylation/decarboxylation pathways present in C_4 plants also most likely occur in CAM plants (only the NADP malic enzyme pathway is shown in Fig. 2), so 1 or 2 ATP are required per CO_2 for this part of the overall process. CAM plants have the additional expense of actively transporting malate into the central vacuole of chlorenchyma cells at night, which requires 1 ATP per malate (Ting, 1985; Lüttge, 1987), whereas the movement out of the vacuole during the daytime is probably by diffusion. Also, 0·5 ATP per CO_2 is required in CAM plants to synthesize the glucan (Fig. 2) that provides the carbon storage needed to form PEP during the night (Edwards & Walker, 1983).

The fixation of CO_2 into a carbohydrate thus requires 3 ATP and 2 NADPH for C_3 species, 4 or 5 ATP and 2 NADPH for C_4 species, and 5·5 or 6·5 ATP and 2 NADPH for CAM species (Black, 1973; Edwards & Walker, 1983; Salisbury & Ross, 1991; Taiz & Zeiger, 1991; Table 1). Based on representative concentrations of reactants and products for plant cells, the energy requirement to form NADPH by a pair of electrons moving along the pathway for noncyclic electron flow is about 220 kJ mol^{-1} and to form ATP is about 50 kJ mol^{-1} (Nobel, 1991). Thus, the energy requirements per mol of CO_2 incorporated into photosynthetic products are about $(3 \times 50) + (2 \times 220)$ or 590 kJ mol^{-1} for C_3 plants, 640–690 kJ mol^{-1} for C_4 plants, and 715–765 kJ mol^{-1} for CAM plants (Table 1). Thus, CAM plants are 20% less efficient than C_3 plants and 10% less efficient than C_4 plants in terms of such energy costs for CO_2 fixation.

Table 1. *Summary of requirements and energy cost for the three CO_2 fixation pathways*

	C_3	C_4	CAM
Requirements per CO_2			
ATP	3	4–5	5·5–6·5
NADPH	2	2	2
Energy cost (kJ mol^{-1})			
Basic process	590	640–690	715–765
Mean for net process, including photorespiration	867	665	740

4. *Effects of photorespiration*

The above calculations are based on the carboxylase activity of Rubisco, which also exhibits an oxygenase activity. The balance between CO_2 fixation following CO_2 binding at the active site (carboxylase activity) and the eventual CO_2 production following O_2 binding (oxygenase activity), the latter leading to photorespiration, depends on the relative concentrations of O_2 and CO_2 near the enzyme. Because the O_2 concentration in the atmosphere and within leaves (or stems) is relatively constant, Rubisco owes its varying activity to the CO_2 concentration, which varies considerably at the location of Rubisco among plants with the three photosynthetic pathways (Edwards & Walker, 1983). The ratio of oxygenase to carboxylase also depends on temperature, the oxygenase activity becoming progressively more important as the temperature rises (Zelitch, 1971; Pearcy & Ehleringer, 1984).

For C_3 plants, the CO_2 level during the daytime in the intercellular air spaces of leaves is about 260–290 μmol mol^{-1} (μmol mol^{-1} equals ppm on a mol fraction or a volume basis; Nobel, 1991). This CO_2 level causes the oxygenase activity of Rubisco to be approximately 25% of the carboxylase activity at temperatures near 25 °C, and an even greater reduction of the carboxylase activity occurs at higher temperatures (Zelitch, 1971; Black, 1973; Osmond, Winter & Ziegler, 1982; Miziorko & Lorimer, 1983). The 590 kJ mol^{-1} CO_2 cost for C_3 plants via the photosynthetic carbon reduction cycle thus leads to the net fixation of only about 0.875 mol CO_2 when the oxygenase activity of Rubisco is 25% of the carboxylase activity, as the photorespiratory cycle releases about 0.5 CO_2 per O_2. Additional energetic costs are involved in the complete photorespiratory cycle, which involves various biochemical pathways in the chloroplasts, peroxisomes, mitochondria, and cytosol and which can release CO_2 at more than one location (Edwards & Walker, 1983; Gregory, 1989; Nobel, 1991; Salisbury & Ross, 1991; Taiz & Zeiger, 1991). For each CO_2 released, on average these reactions require about 5 ATP and 5 NADPH (or NADH), which represents 1350 kJ mol^{-1} and raises the cost by 169 kJ for the net fixation of 0.875 mol CO_2. Hence, a better estimate of the cost for the C_3 pathway is $(590+169)/0.875$ or 867 kJ for the net fixation of 1 mol of CO_2. Another calculation based on specific biochemical reactions indicates that C_3 plants require 4.67 ATP and 3.00 NADPH or 894 kJ mol^{-1} for net CO_2 fixation when the oxygenase activity of Rubisco is 29% of its carboxylase activity (Edwards & Walker, 1983). For an oxygenase activity at 25% of the carboxylase activity as used here, estimates of the average cost per CO_2 fixed for C_3 plants range from 4.26 ATP and 2.86 NADPH or 842 kJ mol^{-1} (Gregory, 1989) to 4.12 ATP and 3.09 NADPH or 885 kJ mol^{-1} (Taiz & Zeiger, 1991).

The intercellular CO_2 levels for C_4 and CAM plants, which influence the ratio of carboxylase to oxygenase activity of Rubisco during the daytime, are harder to determine. The CO_2 levels have been estimated to exceed 1500 μmol mol^{-1} in the bundle sheath cells of C_4 plants (Ehleringer & Björkman, 1977) and have been measured at over 5000 μmol mol^{-1} for various CAM species (Cockburn, Ting & Sternberg, 1979; Spalding *et al.*, 1979). In either case, the oxygenase activity of Rubisco would be relatively small, so the energetic estimates for CO_2 fixation would be little changed by photorespiration (Osmond *et al.*, 1982). Thus, the energetic costs per CO_2 fixed might average 867 kJ mol^{-1} for C_3 plants, 665 kJ mol^{-1} for C_4 plants, and 740 kJ mol^{-1} for CAM plants (Table 1). Consequently, under O_2 and CO_2 levels realistic to present field conditions, CAM plants might operate 10% less efficiently than C_4 plants but 15% more efficiently than C_3 plants with respect to the cost for CO_2 fixation. As the atmospheric CO_2 level increases, currently at a rate of 2 μmol mol^{-1} yr^{-1} (Cure & Acock, 1986; Sasek & Strain, 1990; Nobel, 1991), the relative disadvantage of the C_3 pathway will decrease.

III. CO_2 UPTAKE RATES

1. *Theoretical limits*

The maximal rate of net CO_2 uptake is dictated by the maximal rate of energy supply and the cellular and biochemical processing time per CO_2 incorporated into a photosynthetic product. For C_3 and C_4 plants, energy supply is nearly synonymous with photosynthetic photon flux density (PPFD; wavelengths of 400–700 nm), which has a maximum of about 2000 μmol m^{-2} s^{-1} when the

sun is directly overhead on a clear day (Nobel, 1991). If all the incident photons were used for photosynthesis and the minimum requirement for C_3 plants of 8 photons per CO_2 fixed were achieved, then the maximal rate of CO_2 uptake would be 250 μmol m^{-2} s^{-1}. However, a maximum of only about 80 % of the PPFD is absorbed by photosynthetic pigments (Ehleringer, Björkman & Mooney, 1976; Gifford *et al.*, 1984; Nobel, 1991), lowering the maximal CO_2 uptake rate to about 200 μmol m^{-2} s^{-1}.

Of even greater concern than the PPFD is the processing time for the photochemical events at a reaction centre and for the subsequent steps of photosynthesis leading to CO_2 fixation, which is about 5 ms (Gregory, 1989; Nobel, 1991). Thus, most of the photons incident on the upper part of a horizontal leaf with the sun directly overhead are arriving too fast to be processed by the photosynthetic reactions. Specifically, the excitation frequency at a PPFD of 2000 μmol m^{-2} s^{-1} is about 10 photons absorbed s^{-1} (chlorophyll molecule)$^{-1}$ (Radmer & Kok, 1977; Nobel, 1991). For a processing time of 5 ms and 250 chlorophyll molecules per reaction centre, 2500 excitations occur per second at a PPFD of 2000 μmol m^{-2} s^{-1}, of which only 200 s^{-1} can be processed (5 ms per excitation corresponds to 200 excitations processed per s). Hence, 200/2500 or only 1 in 12·5 excitations (8 %) can be processed. On the other hand, at a much lower PPFD of 200 μmol m^{-2} s^{-1}, the excitation frequency for a reaction centre is 250 s^{-1}, of which again 200 s^{-1} can be processed, which is then 80 % of the incident PPFD.

To help appreciate the limitations on maximal CO_2 uptake rates caused by the processing time, photon absorption and processing will be considered through sequential layers within and among leaves exposed to a high PPFD (2000 μmol m^{-2} s^{-1}), a moderately high PPFD (1200 μmol m^{-2} s^{-1}), and a typical PPFD (300 μmol m^{-2} s^{-1}) at the leaf surface (Table 2). The leaves will be assumed to reflect 10 % of the incident PPFD and to transmit 5 %, both representative values (Ehleringer *et al.*, 1976; Gifford *et al.*, 1984; Nobel, 1991). For purposes of calculation, 10 % of the incident PPFD will be assumed to be absorbed in each of the first 8 layers and the remaining 5 % in the last layer (layers thus refer to PPFD absorption intervals, not cells or leaves). Also, 10 % of the PPFD absorbed by each layer will be assumed to be absorbed by nonphotosynthetic pigments or to be absorbed by accessory pigments such as carotenoids and chlorophyll *b* but not subsequently transferred to chlorophyll *a*. Ignored in these calculations are variations in the number of chlorophyll molecules per reaction centre, such as a lower number for leaves developing at a high PPFD, which leads to a higher processing efficiency (Nobel, 1991), or light-piping from the palisade mesophyll to the spongy mesophyll, which raises the photosynthetic efficiency by distributing the PPFD more uniformly within a leaf (Cui, Vogelmann & Smith, 1991).

Using the average PPFD in each layer, the model proposed indicates that when a PPFD of 2000 μmol m^{-2} s^{-1} is incident on a leaf, about 1700 μmol m^{-2} s^{-1} can be absorbed, 1530 μmol m^{-2} s^{-1} can lead to excitation of chlorophyll *a*, but only 437 μmol m^{-2} s^{-1} will lead to CO_2 fixation (Table 2). Again assuming 8 photons are required per CO_2 fixed, the associated rate of CO_2 fixation is 437/8 or 55 μmol m^{-2} s^{-1}. The efficiency of photon processing at this high PPFD is thus only about 22 % of the incident photons and 26 % of those absorbed. As the PPFD is lowered to 1200 and 300 μmol m^{-2} s^{-1}, the absorption remains at 85 % of the incident photons (Table 2). However, the percentage of the absorbed photons used to fix CO_2 increases from 26 % at a PPFD of 2000 μmol m^{-2} s^{-1} to 39 % at 1200 to 84 % at 300 μmol m^{-2} s^{-1} (Table 2). This has important consequences for PPFD interception by plant canopies, where a fairly uniform distribution of a typical PPFD among a few leaves at different locations above the ground leads to a higher productivity per unit ground area than a moderately high PPFD absorbed by the top leaf of a canopy.

2. *Measured instantaneous values*

How do measured rates of net CO_2 uptake under optimal conditions compare with the predicted maximal net CO_2 uptake rate of about 55 μmol m^{-2} s^{-1}? Measured maximal photosynthetic rates are generally about 20–30 μmol m^{-2} s^{-1} for C_3 plants such as *Glycine max* and *Gossypium hirsutum* and 40–50 μmol m^{-2} s^{-1} for C_4 plants such as *Saccharum officinarum* and *Zea mays* (Black, 1973; Radmer & Kok, 1977; Winter, 1985; Salisbury & Ross, 1991). However, even higher values

Table 2. *Attenuation of PPFD through leaves, indicating the absorbed PPFD leading to CO_2 fixation in each layer, for three ambient PPFD levels*

Available	Absorbed by layer	Leading to chl a excitation	Leading to CO_2 fixation
PPFD (2000 μmol m^{-2} s^{-1})			
1800	200	180	19
1600	200	180	21
1400	200	180	25
1200	200	180	29
1000	200	180	36
800	200	180	46
600	200	180	64
400	200	180	107
200	100	90	90
100			
Total	1700	1530	437
PPFD (1200 μmol m^{-2} s^{-1})			
1080	120	108	19
960	120	108	21
840	120	108	25
720	120	108	29
600	120	108	36
480	120	108	46
360	120	108	64
240	120	108	107
120	60	54	54
60			
Total	1020	918	401
PPFD (300 μmol m^{-2} s^{-1})			
270	30	27	19
240	30	27	21
210	30	27	25
180	30	27	27
150	30	27	27
120	30	27	27
90	30	27	27
60	30	27	27
30	15	14	14
15			
Total	255	230	214

The leaves were assumed to reflect 10% of the incident PPFD, to transmit 5% (Ehleringer *et al.*, 1976; Gifford *et al.*, 1984; Nobel, 1991), and to lose 10% of the PPFD absorbed in each of the 9 layers to non-photosynthetic processes (sequential layers can be in the same leaf or in different leaves, depending on leaf anatomy and canopy architecture). The excitation frequency at a PPFD of 2000 mol m^{-2} s^{-1} was assumed to be 10 photons absorbed s^{-1} chlorophyll^{-1} and the absorbed photons were assumed to be processed in 5 ms per reaction centre containing 250 chlorophylls (Radmer & Kok, 1977; Gregory, 1989; Nobel 1991).

sometimes occur. For instance, under field conditions with the sun directly overhead, the maximal net CO_2 uptake rate for six C_3 species with the highest rates averages 48 μmol m^{-2} s^{-1} and for six such C_4 species averages 64 μmol m^{-2} s^{-1} (Table 3). These rates are generally consistent with the arguments in the previous section based on the maximal PPFD and the photon processing time. Also, these exceptionally high values indicate that the maximal rates of net CO_2 uptake are lower

Table 3. *Maximal instantaneous rates of net CO_2 uptake for leaves of C_3 and C_4 plants*

Pathway	Species	Maximal rate of net CO_2 uptake (μmol m^{-2} s^{-1})	Reference
C_3	*Cammissonia claviformis*	56–59	Mooney *et al.* (1976); Longstreth *et al.* (1980)
	Gossypium hirsutum	43	Osmond *et al.* (1982)
	Medicago sativa	54	Gifford (1974)
	Oenothera elata	42	Longstreth *et al.* (1980)
	Triticum boeoticum	45	Gifford (1974)
	Typha latifolia	43	Zelitch (1971)
C_4	*Amaranthus palmeri*	75	Pearcy & Ehleringer (1984)
	A. retroflexus	65	Longstreth *et al.* (1980)
	Hilaria rigida	66	Nobel (1980*a*)
	Saccharum hybrid	64	Gifford (1974)
	Sorghum sudanense	57	Gifford (1974)
	Zea mays	59	Osmond *et al.* (1982)

Data are for sustainable rates of net CO_2 flow into both leaf surfaces and are expressed on the basis of projected leaf area (one side of the leaves) for leaves exposed to a PPFD of about 2000 μmol m^{-2} s^{-1} at 21 % O_2 and 0·034 % CO_2 (or adjusted to this condition where appropriate data were available).

for C_3 plants than for C_4 plants. Specifically, the ratio of maximal net CO_2 uptake rates for the six C_3 species to the rates for the six C_4 species is 0·74 (Table 3) compared with a ratio of 0·77 predicted based on the relative energy costs of these two pathways at about 25 °C under present CO_2 concentrations.

The situation for the maximal net CO_2 uptake rates of CAM plants is less clear. Much fewer such measurements have been made than for C_3 and C_4 plants, and net CO_2 uptake measurements for CAM plants are often expressed on a total surface area basis, as is appropriate for opaque 3-D objects such as a cactus stem or an agave leaf (Nobel, 1988). For example, an agave leaf can be approximately triangular in cross section, the upper (adaxial) surface having 10–15 % less surface area than the lower surface. If the data are expressed on the basis of projected leaf (or stem) area, as for C_3 and C_4 plants, maximal net CO_2 uptake rates at night for CAM plants include 23 μmol m^{-2} s^{-1} for *Agave fourcroydes* (Nobel, 1985) and *Opuntia ficus-indica* (Nobel & Hartsock, 1983, 1984). Recently, nocturnal net CO_2 uptake rates of 29 μmol m^{-2} s^{-1} for *Agave salmiana* and 34 μmol m^{-2} s^{-1} for *Agave mapisaga* have been measured (Nobel, García-Moya & Quero, 1992). Hence, at least some CAM plants can achieve similar maximal net CO_2 uptake rates as most C_3 and C_4 plants, although not the highest rates of certain species (Table 3). However, the rates for CAM plants represent CO_2 uptake at night and thus are not analogous to the instantaneous rates for C_3 and C_4 plants exposed at that time to a PPFD of 2000 μmol m^{-2} s^{-1}.

3. *Integrated daily values*

Of more relevance to productivity than instantaneous rates of net CO_2 uptake at a particular PPFD is the integrated amount of net CO_2 uptake over a 24 h period. This includes the effect of CO_2 loss by respiration, which can consume 10–30 % or more of the CO_2 fixed during the daytime (Zelitch, 1971; Monteith, 1977; Nobel, 1991; Salisbury & Ross, 1991). Surprisingly few values of integrated net CO_2 uptake over 24 h periods are published for leaves of C_3 and C_4 plants.

If the net CO_2 uptake rate were to increase linearly from 0 μmol m^{-2} s^{-1} at dawn to 55 μmol m^{-2} s^{-1} at noon and then decrease linearly back to 0 at dusk for a 12 h daytime, the total net CO_2 uptake over the daytime would be 1188 mmol m^{-2} d^{-1}. As another alternative, the approximately sinusoidal variation in daily PPFD could be represented, for purposes of calculation, by a square wave with a magnitude of 2000 μmol m^{-2} s^{-1} (the maximal PPFD) for 8 h d^{-1}; predicted net CO_2 uptake during the daytime would then be 1584 mmol m^{-2} d^{-1} for such

Table 4. *Maximal net CO_2 uptake over 24 h periods for CAM plants*

Species	Net CO_2 uptake (mmol m^{-2} d^{-1})	Reference
Agave fourcroydes	760	Nobel (1985)
A. mapisaga	1170	Nobel *et al.* (1991)
A. salmiana	1053	Nobel *et al.* (1991)
A. tequilana	700	Nobel & Valenzuela (1987)
Opuntia ficus-indica	1081	Nobel & Hartsock (1983, 1984)

Data are expressed on the basis of projected organ area for well-watered plants, optimal temperatures, and clear days.

a C_3 or C_4 plant. If 10 % of the carbon acquired during the daytime were lost by the leaves by respiration at night (119 and 158 mmol m^{-2} d^{-1} for these two cases), the net CO_2 uptake under these two optimal conditions would be 1069 and 1426 mmol m^{-2} d^{-1}, respectively. By way of comparison, net CO_2 uptake over 24 h periods has been measured for various CAM species (Nobel, 1988). When expressed per unit projected area, total daily net CO_2 uptake averages 953 mmol m^{-2} d^{-1} for five CAM species (Table 4), with a maximum value of 1170 mmol m^{-2} d^{-1}. Again the conclusion is reached that under optimal conditions, CAM plants can have a net CO_2 uptake on a daily basis that is similar to values for C_3 and C_4 plants.

Instead of using net CO_2 uptake measured over 24 h periods, the integrated daily values for CAM plants are often expressed indirectly using the nocturnal increase in acidity. For instance, the nocturnal acidity increase on a projected area basis is 2680 mmol H^+ m^{-2} for *Opuntia ficus-indica* (Nobel & Hartsock, 1983), 1860 mmol m^{-2} for *Agave salmiana* (Nobel, 1988), 1520 mmol m^{-2} for *Opuntia chlorotica* (Nobel, 1980b), and 1500 mmol m^{-2} for *Opuntia stricta* (Osmond, Nott & Firth, 1979). Using 2 H^+ per malate and hence per CO_2 incorporated (Lüttge & Ball, 1980; Nobel, 1988), such values range from 750 to 1340 mmol CO_2 m^{-2}. However, nocturnal acidity increases reflect both net CO_2 uptake from the atmosphere and also refixation of CO_2 released internally by respiration (Fig. 2). Moreover, possible net CO_2 uptake during the daytime is not included in nocturnal acidity changes. Sometimes nocturnal acidity increases are expressed on the basis of nocturnal increases in osmotic pressure or in concentration of malate and other organic acids (Smith *et al.*, 1986; Nobel, 1988), but this is even less useful for assessing productivity, as it is highly influenced by the thickness of the chlorenchyma and hence by the ability to store organic acids per unit surface area.

4. *Water-use efficiency*

Water-use efficiency (WUE) refers to the ratio of CO_2 fixed to water lost, which varies considerably among the three photosynthetic pathways. Although WUE depends on environmental conditions such as the partial pressure of water vapour in the atmosphere as well as plant properties such as leaf age, representative values can be indicated. Integrated over 24 h periods, WUE generally averages 0·5–1·5 mmol CO_2 (mol H_2O)$^{-1}$ for mature leaves of C_3 plants, 1·0–2·0 for C_4 plants, and 4–10 for CAM plants (Szarek & Ting, 1975; Osmond, Björkman & Anderson, 1980; Le Houérou, 1984; Nobel, 1991). Clearly, the stomatal opening predominantly at night, when leaf and stem temperatures are lower than during the daytime, leads to less water loss by CAM plants per mol of CO_2 taken up than for leaves of C_3 and C_4 plants.

A higher WUE is of no particular advantage when water is readily available to the plants. However, sometime during a day, season, or year, water becomes limiting for net CO_2 uptake for nearly all crops and in nearly all habitats. At such times, CAM plants can have a greater net CO_2 uptake per unit leaf or stem area than do C_3 and C_4 plants. Moreover, many CAM plants are succulent and can store considerable amounts of water in their shoots. Such water storage plus the high WUE associated with CAM can greatly extend the periods for substantial net CO_2 uptake. For instance, when plant water uptake is prevented because the soil has a lower water potential than the plant, appreciable nocturnal stomatal opening leading to at least half of maximal net CO_2

uptake can occur for about 22 d for *Opuntia ficus-indica* and 29 d for *Ferocactus acanthodes* (Nobel, 1977, 1988).

IV. CANOPY ARCHITECTURE AND LIGHT ABSORPTION

1. *Basic attributes*

Plant productivity depends on the orientation of leaves in space as well as on the net CO_2 uptake rate as a function of incident PPFD for such leaves. The latter has received greater attention among plant physiologists, whereas the former may actually be more important for productivity of plant canopies (Zelitch, 1971; Gifford *et al.*, 1984; Lambers, 1987; Wardlaw, 1990; Nobel, 1991). Certain plant architectures maximize light interception over the course of a day and hence tend to maximize productivity per unit ground area. Besides net carbon gain by the leaves, respiration by both roots and stems as well as their construction costs must be included when plant productivity is considered. Highly simplified calculations will be employed here to highlight the principles involved, detailed analyses being readily available (Loomis & Gerakis, 1975; Monteith, 1977; Jarvis & Leverenz, 1983; Loomis, 1983; Russell, Marshall & Jarvis, 1989; Nobel, 1991).

The simplest plant canopy to consider consists of an infinitely large horizontal leaf, or a layer of touching leaves. Because of effects of cloudiness, latitude, and the variation of the sun's trajectory during a year, the average daily maximal PPFD on a horizontal surface will be assumed to be 1200 μmol m^{-2} s^{-1}, resulting in a PPFD leading to CO_2 fixation of 401 μmol m^{-2} s^{-1} (Table 2). Assuming 8 photons are required per CO_2 fixed, the net CO_2 uptake rate is 401/8 or 50 μmol m^{-2} s^{-1}. If such a maximal rate occurred for 8 h each day, the net CO_2 uptake during the daytime for this leaf would be 1440 mmol m^{-2}. A night-time respiration of 158 mmol m^{-2}, as previously calculated for this leaf, will be assumed. For purposes of calculation, the same additional carbon costs will be assumed for the stem and for the roots; such costs can represent maintenance respiration, growth respiration, and carbon structurally incorporated into these organs. Thus, the net carbon gain that can be used for aboveground productivity in this simple model is $1440 - (3 \times 158)$ or 966 mmol m^{-2} d^{-1}, which is 353 mol m^{-2} yr^{-1}. How much biomass does this represent? Plant dry weight consists of about 47 % carbon in the non-ash fraction, which is about 95 % of the dry weight, so carbon represents about 45 % of the total dry weight (Lieth & Whittaker, 1975; Williams *et al.*, 1987; Salisbury & Ross, 1991). Thus, the annual net aboveground productivity per unit ground area represents (353 mol m^{-2} yr^{-1}) (12 g mol^{-1}) (1/0·45) or 9·41 kg d. wt m^{-2} yr^{-1}. The conventional unit for agricultural productivity is a metric ton or tonne (1000 kg or 1 Mg) per hectare (10000 m^2) per year; Mg and hectare will be used here. In this unit the maximum productivity expected is 94 Mg ha^{-1} yr^{-1} (9·4 kg m^{-2} yr^{-1}).

Canopies generally consist of multiple layers of leaves. If a second horizontal leaf layer occurred under the canopy just considered, the incident PPFD on it would be about 60 μmol m^{-2} s^{-1} (assuming a 5 % transmittance, as above; see Table 2), which under the previous assumptions would lead to a net CO_2 uptake rate of 5·7 μmol m^{-2} s^{-1}, or 165 mmol m^{-2} for an 8 h daytime at such a PPFD. However, the respiration by this leaf layer at night plus the stem and the root respiration lead to no carbon gain (actually, a net carbon loss). On the other hand, a canopy of four layers of leaves oriented in such a way that each layer receives one-quarter of the available PPFD, or 300 μmol m^{-2} s^{-1}, can lead to more CO_2 uptake than the single-layer canopy. The net rate of CO_2 uptake for such leaves would be 214/8 or 27 μmol m^{-2} s^{-1} (Table 2), which leads to 770 mmol m^{-2} for an 8 h daytime. Assuming the same respiration rate as before (158 mmol m^{-2} for the leaf, the supporting stem, and the associated roots for each leaf layer), the net gain would be $770 - (3 \times 158)$ or 296 mmol m^{-2} d^{-1} for each leaf layer, leading to 1184 mmol m^{-2} d^{-1} overall for the four leaf layers, which is 23 % higher than for the canopy consisting of a single, horizontal leaf. The annual aboveground dry-weight productivity of this idealized four-layer canopy is 115 Mg ha^{-1} yr^{-1}.

The above productivity calculations involve many assumptions and conditions. For instance, if the PPFD were increased by 100 μmol m^{-2} s^{-1} on one leaf layer in the four-layer canopy and decreased by the same amount on another layer, the annual productivity would decrease by 6 % to 108 Mg ha^{-1} yr^{-1}. Eight photons are assumed to be required per CO_2 fixed for each of the

photosynthetic pathways. The calculations assume no limitation on CO_2 entry into the leaves by stomata and no limitation on photosynthesis by starch synthesis or temporary overburdening of the phloem delivery system for photosynthetic products (Wardlaw, 1990). None of the incident PPFD is assumed to be incident on nonphotosynthetic stems or standing dead material. Also, very little PPFD can strike the soil and hence be unavailable for photosynthesis, which also means very little ground area can be involved with the passageways necessary for crop management. Moreover, no allowance is made for limitations on net CO_2 uptake caused by drought, non-optimal temperatures (which occur part of every day, as well as seasonally), overcast days, or nutrient stress. The costs for nitrate reduction are also not included. These physiological and environmental factors substantially reduce maximal productivity from the 100 or so $Mg\ ha^{-1}\ yr^{-1}$ predicted for year-round optimal conditions.

2. Integration using an environmental productivity index

(a) *Definitions.* The influence of environmental factors such as water status, temperature, and PPFD on net CO_2 uptake by leaves and by photosynthetic stems over 24 h periods can be quantitatively described using EPI (Nobel, 1984, 1988). First, the relationship between net CO_2 uptake per unit shoot surface area over 24 h periods and some environmental variable is determined in the laboratory while varying one environmental factor at a time. For instance, the water index indicates the fractional limitation on net CO_2 uptake caused by soil water status. It has a value of 1 for plants in wet soil and decreases to zero during a prolonged drought that causes complete stomatal closure. Drought, which is defined as commencing when a plant can no longer obtain water from the soil and hence must rely on its own reserves of stored water, causes a decrease in the maximal rate of net CO_2 uptake by CAM plants, progressively eliminates any daytime net CO_2 uptake, and shifts the time for maximal nocturnal net CO_2 uptake to later times in the night (Nobel, 1977, 1988). For *Agave deserti*, the maximal rate of net CO_2 uptake occurs at the beginning of the night under well-watered conditions, near midnight after 9 d of drought, and at 2 h before dawn after 33 d of drought; compared with the wet condition, net CO_2 uptake over 24 h periods decreases 64 % after 9 d of drought and becomes zero after 33 d of drought (Nobel, 1984, 1990). Thus, its water index is 1·00 under well-watered conditions, becoming 0·36 after 9 d of drought and 0·00 after 33 d.

Net CO_2 uptake over 24 h for many CAM plants is optimal for day/night air temperatures of about 25 °C/15 °C (Kluge & Ting, 1978; Nobel, 1988). Actually, total daily net CO_2 uptake for CAM plants is determined primarily by temperatures at night, when most CO_2 uptake occurs, so the temperature index can be related to the average night-time temperatures or to the minimum night-time temperatures. For *A. deserti*, net CO_2 uptake over 24 h periods is 16 % lower at an average night-time temperature of 5 °C and 33 % lower at 25°C compared with 15 °C (Nobel, 1984); such laboratory studies, which maintained the plants at a given temperature for 2 wk to allow temperature acclimation to occur, indicate a temperature index for *A. deserti* of 0·84 at an average night-time temperature of 5 °C, 1·00 at 15 °C, and 0·67 at 25 °C (Nobel, 1984). Likewise, a PPFD index can be determined after maintaining the plants for 7–10 d at a particular total daily PPFD to allow the glucan, associated compounds, and the enzymes (Fig. 2) to achieve comparable day-to-day levels; again for *A. deserti*, the PPFD index is 0·00 at a low total daily PPFD of 3 $mol\ m^{-2}\ d^{-1}$ (the light compensation value on a 24 h basis), 0·50 at 11 $mol\ m^{-2}\ d^{-1}$, 0·90 at 22 $mol\ m^{-2}\ d^{-1}$, and 1·00 at 37 $mol\ m^{-2}\ d^{-1}$ (the PPFD saturation value; Nobel, 1984). For proper adjustment to field conditions, an appropriate range of temperatures must be used for the temperature index and the fluctuating PPFD in the field must be taken into consideration for the PPFD Index (Nobel, 1988; García de Cortázar & Nobel, 1991).

The three component indices are multiplied to obtain EPI:

$$EPI = water\ index \times temperature\ index \times PPFD\ index. \tag{1}$$

EPI represents a first-order approximation of the influence of these three environmental factors on net CO_2 uptake over 24 h and hence on productivity. Because each component index represents the fractional net CO_2 uptake expected for limitations on net CO_2 uptake by that factor, EPI represents

the fraction of maximal net CO_2 uptake expected under particular conditions of soil water status, ambient temperature, and available PPFD. It is 1·00 for well-watered plants at optimal temperatures and saturating PPFD. A multiplicative form is used for EPI, because each of the three environmental factors can independently and simultaneously limit CO_2 uptake. When one component index is zero, such as when stomata remain closed during prolonged drought leading to a water index of 0·00, net CO_2 uptake will then not occur, even under optimal conditions for temperature or PPFD. Second-order interactive effects can occur among the environmental factors in the component indices, but such effects are small over most of the range of each component index (Nobel, 1988).

The influences of soil elements on net CO_2 uptake and productivity can be evaluated by measuring net CO_2 uptake over 24 h periods for an EPI of known value for plants in the particular field-soil of interest, compared with net CO_2 uptake by the plants in the soil used in the laboratory determinations of EPI. Also, a nutrient index can be determined experimentally, as has been done using the extensive data on the influences of soil mineral elements on net CO_2 uptake and growth for agaves and cacti (Nobel, 1989). The influences of only five mineral elements have been documented for more than one species of agaves and cacti, and their nutrient index is as follows (Nobel, 1989):

$$\begin{pmatrix} \text{nutrient} \\ \text{index} \end{pmatrix} = \begin{pmatrix} \text{nitrogen} \\ \text{index} \end{pmatrix} \times \begin{pmatrix} \text{phosphorus} \\ \text{index} \end{pmatrix} \times \begin{pmatrix} \text{potassium} \\ \text{index} \end{pmatrix} \times \begin{pmatrix} \text{boron} \\ \text{index} \end{pmatrix} \times \begin{pmatrix} \text{sodium} \\ \text{index} \end{pmatrix} \qquad (2)$$

An empirical relationship for each component index is based on the soil level for that element and the resulting net CO_2 uptake, growth, or productivity.

(b) *Applications.* Although the development and the initial application of EPI have been with agaves and cacti (Nobel, 1984, 1988), the approach is general and can be applied to any species whose responses of net CO_2 uptake over 24 h periods to water status, temperature, PPFD, and soil mineral elements are systematically measured. Moreover, EPI and especially its component indices are analogous to other indices that have been proposed for quantifying productivity.

Some productivity indices and yield predictions are based only on rainfall and evapotranspiration (Sneva & Hyder, 1962; Chang, 1968; Nix & Fitzpatrick, 1969; Duncan & Woodmansee, 1975; Le Houérou, 1984), although productivity varies more from year to year at a particular site than does rainfall (Le Houérou, Bingham & Skerbek, 1988). Indices for crop performance and forage yields have also been based on the moisture supply and water-holding capacity of soils (Dahl, 1963; Nix & Fitzpatrick, 1969; McBride & Mackintosh, 1984). Developmental stages and growth indices are often based on the accumulated time that the ambient temperature is above some value, the 'degree-day' approach (Castonguay & Dubé, 1985; Long & Woodward, 1988). Crop growth can also be proportional to intercepted radiation (Monteith, 1977; Jones, 1983); for instance, the g dry weight produced by leaves per mol of photons incident has been estimated as from 1·64 (Bugbee & Salisbury, 1988) to 1·78 (Loomis & Williams, 1963) under field conditions, whereas the values for the one- and four-layer canopies considered here are 1·11 and 2·37, respectively, leading to an average of 1·74 g d. wt mol^{-1} of photons. Single-factor approaches have proved extremely useful for specific applications and indeed are simpler to use than is EPI. Yet an integrated approach considering water status, temperature, PPFD, and soil mineral elements, such as is the case for EPI, is much to be preferred for quantitative predictions and analysis of plant productivity (Gifford *et al.*, 1984; Nobel, 1988).

Net CO_2 uptake over 24 h periods is not linearly related to temperature or to radiation, and rainfall has different patterns during months of different years. Errors can therefore arise when average monthly values are used instead of daily values to calculate component indices and EPI (García de Cortázar, Acevedo & Nobel, 1985; Nobel & Hartsock, 1986; Nobel, 1988). Thus, EPI is best calculated day-by-day and the daily values then averaged to predict annual productivity. Also, component indices of EPI can be calculated daily and averaged over a year to help analyse limitations of specific environmental factors on net CO_2 uptake. For instance, twice-monthly irrigation is usually sufficient to maintain the water index at 1·00, where irrigation only in the early summer led to an average water index of 0·79 for *Opuntia ficus-indica* in central Chile (García de

Cortázar *et al.*, 1985). Annual rainfall of 1010 mm led to an average water index of 0·81 for *Agave fourcroydes* in eastern Mexico (Nobel, 1985), and an annual rainfall of 1080 mm led to a water index of 0·53 for *A. tequilana* in western Mexico (Nobel & Valenzuela, 1987). The annual water index for these three CAM plants therefore averaged 0·71. Because of a lower water-use efficiency for non-succulent C_3 and C_4 plants, their average water index is lower than for CAM plants, and a value of 0·60 will be assumed here for purposes of calculation. For the three CAM species, the temperature index calculated daily and averaged over a year was 0·85 for *A. fourcroydes*, 0·84 for *A. tequilana*, and 0·90 for *O. ficus-indica*. Thus, the temperature index averaged 0·86. The temperature index for C_3 and C_4 plants under the same field conditions would be expected to be lower, possibly about 0·80, as a low net CO_2 uptake at one part of the night (often the beginning) is usually compensated for by a higher uptake during other parts for CAM plants, whereas net CO_2 uptake for C_3 and C_4 plants tends to respond to the temperature occurring at a particular time (the higher temperature optimum for photosynthesis by C_4 compared with C_3 plants is also important; Pearcy & Ehleringer, 1984).

In contrast to responses of net CO_2 uptake for plants in the field to temperature and to rainfall plus irrigation, which can be estimated based on measured values for these environmental factors, the response of net CO_2 uptake to PPFD depends on canopy architecture, which is a partly controllable feature in agriculture that varies with plant spacing as well as size, so it deserves a separate consideration in the next section. Yet a temperature index of 0·80 by itself would reduce the average maximal productivity calculated in the previous section (about 105 Mg ha^{-1} yr^{-1}) to 84 Mg ha^{-1} yr^{-1} for C_3 and C_4 plants. Without year-round irrigation and so using a water index of 0·60 to provide an estimate, the maximal productivity would be about 50 Mg ha^{-1} yr^{-1}. Soil nutrient limitations would reduce annual productivity even more. Thus, 50 Mg ha^{-1} yr^{-1} should be considered a benchmark against which maximal productivities are judged for plants from all three photosynthetic pathways. For instance, the maximum productivity predicted for a C_3 crop having a complete canopy throughout the year in England, with photosynthesis not reduced by low temperatures in the winter or by drought in the summer, is 54 Mg ha^{-1} yr^{-1} (Monteith, 1977).

3. *Leaf and stem area indices*

The leaf area index (LAI; leaf surface area per unit ground area) and the stem area index (SAI; stem surface area per unit ground area) affect net CO_2 uptake for a plant canopy. Such parameters depend largely on plant spacing and hence can be altered by management practices. Because the leaves and the stems of CAM plants tend to be opaque, one side is independent of the other with respect to the interception of PPFD, so shoot area will henceforth be on a total surface area basis, with each surface orientation considered separately.

To determine the PPFD intercepted by the complex array of surfaces making up the shoot of a CAM plant, a ray-tracing technique (Fig. 3) has proved useful (García de Cortázar *et al.*, 1985; Nobel & García de Cortázar, 1987). This model permits an accurate calculation of radiation interception and shadows cast by a set of planar surfaces whose Cartesian coordinates are known, such as when each plant surface is subdivided into specific smaller areas. For instance, the shoot of a platyopuntia containing 27 cladodes has been divided into 5000 subsurfaces (García de Cortázar *et al.*, 1985), and the basal rosette of leaves for an agave with 160 leaves has been divided into 100 000 subsurfaces (Nobel & García de Cortázar, 1987). The direct solar beam is divided into a similar number of equally spaced parallel sub-beams; diffuse radiation is assumed to be isotropic, and view factors are included to correct for the occlusion by other parts of the shoot of diffuse radiation from the sky and radiation reflected from the soil surface. After briefly describing the model, it will be used to predict productivity for two CAM species.

When a particular sub-beam is intercepted by a subsurface (e.g. sub-beam A in Fig. 3), the angle between the normal to its surface and the solar sub-beam is determined so that the incident direct PPFD can be calculated. If that sub-beam subsequently strikes a second surface, then the latter surface is in the shadow of the former surface. If the sub-beam does not strike any subsurface of the shoot, then it may reach the ground (sub-beam B) and lead to diffuse radiation reflected from the soil surface. A sub-beam may pass through one plant unintercepted (sub-beam C in Fig. 3) but
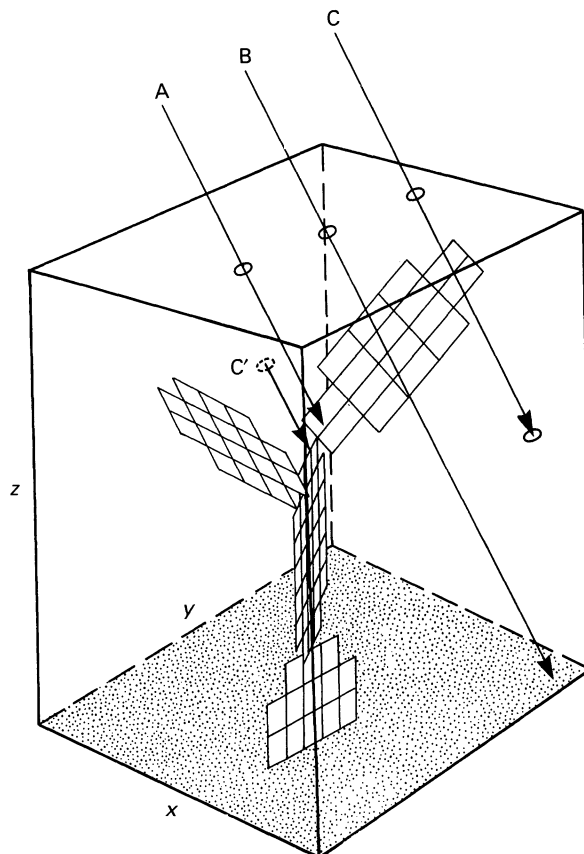
Figure 3. Schematic illustration of a platyopuntia with four cladodes, whose surfaces are divided into squares. Direct PPFD is indicated by sub-beams that are incident on a cladode (sub-beam A), incident on the ground (sub-beam B), or not intercepted by the plant or the ground (sub-beam C). The ray-tracing model allows sub-beam C to be incident on an adjacent identical plant, which is geometrically equivalent to approaching the original plant at the opposite side but at the same height and the same angle as for the exit of sub-beam C (represented by sub-beam C', which strikes the lower part of the plant). Used by permission from García de Cortázar *et al.* (1985) (© Elsevier Science Publishers B.V.).

strike a subsurface on an adjacent plant (sub-beam C'). The probability for such interception by a second plant depends on the interplant spacing, a parameter that can be varied in the ray-tracing model. The number of times a day that are simulated as well as the ambient environmental conditions, such as cloud cover, can also be varied. The PPFD on a particular subsurface is integrated over the daytime to determine the total daily PPFD intercepted. Based on the response of total daily net CO_2 uptake to total daily PPFD, the PPFD index is calculated for each subsurface. The model also determines the water and the temperature indices so that EPI [see eqn (1)] can be calculated for each subsurface. EPI times the maximal daily net CO_2 uptake under optimal conditions (EPI = 1·00) gives the predicted net CO_2 uptake for that subsurface, which can then be summed for all subsurfaces and expressed per unit ground area. Such daily net CO_2 uptake can be corrected for respiration, converted to dry weight, and then integrated over the year to estimate the annual productivity.

The ray-tracing model will be used here to predict productivity as a function of LAI for an agave and as a function of SAI for a platyopuntia (Fig. 4). Environmental data for *Agave fourcroydes* Lem. (Agavaceae) are based on a study near Mérida, Yucatán, Mexico (Nobel, 1985; Nobel & García de Cortázar, 1987) and for *Opuntia ficus-indica* (L.) Miller (Cactaceae) on a study near Santiago, Chile (Acevedo, Badilla & Nobel, 1983; García de Cortázar *et al.*, 1985). The EPI approach incorporates laboratory measurements of CO_2 responses for *A. fourcroydes* (Nobel, 1985) and *O. ficus-indica* (Nobel & Hartsock, 1983, 1984). Respiration for the roots and the non-photosynthetic parts of the shoot as well as the overall carbon structural costs will be assumed to equal 20% of the maximal daily net CO_2 uptake per unit leaf or stem surface area and to be
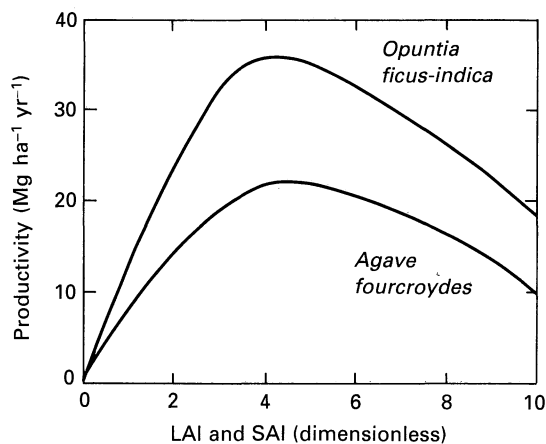
Figure 4. Predicted annual above-ground dry weight productivities for two CAM species, *Agave fourcroydes* and *Opuntia ficus-indica*. A ray-tracing technique was used to predict PPFD interception by subsurfaces of the shoot (García de Cortázar *et al.*, 1985; Nobel & García de Cortázar, 1987). CO_2 responses to environmental factors measured in the laboratory were used to determine EPI expressed under field conditions, and corrections were made for carbon costs of the shoot and the root. Environmental data are for Mérida, Yucatán, Mexico (*A. fourcroydes*) and Til Til, near Santiago, Chile (*O. ficus-indica*).

proportional to plant biomass, as above (respiration for the photosynthetic part of the shoot is already included, as EPI is based on net CO_2 uptake over 24 h periods). For both species, simulated annual productivity increases as the shoot area per unit ground area increases; productivity is maximal for an LAI of 4–5 for *A. fourcroydes* and for an SAI of about 4 for *O. ficus-indica* (Fig. 4). Maximal annual above-ground dry-weight productivity is predicted to be 22 Mg ha^{-1} yr^{-1} for *A. fourcroydes* and 36 Mg ha^{-1} yr^{-1} for *O. ficus-indica*. Annual productivity decreases as the shoot surface area per unit ground area increases above the optimal values, because the structural carbon and respiratory costs then become greater than the net CO_2 uptake by the new plant material. At an LAI or SAI of 10, predicted productivity for *A. fourcroydes* and *O. ficus-indica* decreases to about half of the maximal value (Fig. 4).

V. MEASURED BIOMASS PRODUCTIVITY

1. *Possible values*

So far a benchmark productivity of about 50 Mg ha^{-1} yr^{-1} has been estimated for C_3 or C_4 plants with a high photosynthetic rate (55 μmol m^{-2} s^{-1} in full sunlight) but with realistic temperature and water conditions. Also, productivities of 22 to 36 Mg ha^{-1} yr^{-1} have been simulated for CAM plants at optimal spacings under field conditions (Fig. 4). What productivities are actually achieved? Emphasis is on maximal productivity on an annual basis, which was an active area of research for C_3 and C_4 species in the 1960s and 1970s (Gifford, 1974; Loomis & Gerakis, 1975; Monteith, 1978; Loomis, 1983).

2. *C_3 and C_4 plants*

The productivity of cultivated plants varies considerably, depending on the length of the growing season, whether the plants are annuals or perennials, the particular part of the plant harvested (which influences breeding efforts related to productivity), and other management aspects. Nevertheless certain generalities can be made. For instance, the highest productivities occur for C_4 plants, reaching about 70 Mg ha^{-1} yr^{-1} for *Pennisetum purpureum* and *Saccharum officinarum* (Table 5). Indeed, none of the other highest producers exceed 50 Mg ha^{-1} yr^{-1}. The highest productivities for the six agronomic C_4 species average 49 Mg ha^{-1} yr^{-1} compared with 35 Mg ha^{-1} yr^{-1} for the highest productivities of the six best-producing C_3 species (including the oil palm *Elaeis guineensis*; Table 5). Most such plants are grown as annuals, so growth generally

Table 5. *Annual productivities of highly productive* C_3 *and* C_4 *plants*

Type and species	Location	Productivity ($Mg\ ha^{-1}\ yr^{-1}$)	Reference
C_3 (agricultural crops)			
Beta vulgaris	California, USA	30–34	Loomis & Gerakis (1975)
Elaeis guineensis	Malaysia	40	Cooper (1975)
Lolium perenne	England	29	Gifford (1974)
Manihot esculenta	Java; Sierra Leone	33–45	Loomis & Gerakis (1975); Loomis (1983)
Medicago sativa	Arizona and California, USA	30–34	Loomis, Williams & Hall (1971); Loomis & Gerakis (1975)
Triticum aestivum	Washington, USA	30	Loomis & Gerakis (1975)
C_4 (agricultural crops)			
Cynodon dactylon	California, USA	32	Loomis & Gerakis (1975)
C. plectostachyus	Puerto Rico	37	Loomis & Gerakis (1975)
Pennisetum purpureum	El Salvador; Puerto Rico	70	Loomis & Gerakis (1975); Loomis (1983)
Saccharum officinarum	Guyana; Hawaii, USA; Queensland, Australia	50–67	Evans 1975; Loomis & Gerakis (1975); Beadle *et al.* (1985)
Sorghum bicolor	California, USA	47	Loomis & Gerakis (1975)
Zea mays	Egypt; Italy; Peru; Colorado and California, USA	26–40	Cooper (1975); Loomis & Gerakis (1975)
C_3 (trees)			
Cryptomeria japonica	Japan	44	Kira (1975)
Eucalyptus globulus	Portugal	40	Jarvis & Leverenz (1983)
E. grandis	South Africa	41	Schönau & Pennefather (1975)
Pinus radiata	New Zealand	34–38	Miller (1971); Madgwick (1981)
Salix purpurea	New Zealand	36	Jarvis & Leverenz (1983)
Tsuga heterophylla	Oregon, USA	36	Fujimori (1971)

Productivities are above-ground only, except for *Beta vulgaris* and *Manihot esculenta*. Data represent high but sustainable dry-weight yields for sufficiently large and uniform fields that avoid border effects (higher productivities per unit area on the periphery), with the possible exception of *Pennisetum purpureum* (Loomis & Gerakis, 1975; Monteith, 1978; Loomis, 1983), for which field data have been adjusted accordingly (1 Mg = 1000 kg = 1 tonne).

occurs over only part of the year. The average maximum productivity of the six best-producing C_3 tree species is 39 $Mg\ ha^{-1}\ yr^{-1}$ (Table 5). The latter plants are perennials with closed canopies essentially year-round and thus are more appropriate for comparison with plantations of perennial CAM plants.

3. CAM plants

Annual above-ground productivities have been determined for more than one dozen species of CAM plants, with values ranging widely (Nobel, 1988), just as for C_3 and C_4 plants. For the five most productive species under agricultural conditions, the annual productivity averages 26 $Mg\ ha^{-1}\ yr^{-1}$, including 35 $Mg\ ha^{-1}\ yr^{-1}$ for *Ananas comosus* (pineapple; Table 6). Such average values exceed the annual productivities of common C_3 agronomic crops such as *Glycine max*, *Hordeum vulgare*, *Oryza sativa*, *Pisum sativum*, and *Solanum tuberosum* (Cooper, 1975; Loomis & Gerakis, 1975; Beadle *et al.*, 1985) as well as the productivities of nearly all forests, both deciduous and evergreen (Kira, 1975; Jarvis & Leverenz, 1983). Moreover, because of nocturnal stomatal opening and its associated high WUE, the productivities of these highly productive CAM plants are often achieved in regions of only modest annual rainfall. For the five species considered (Table 6), the annual rainfall for the times when productivity was measured averaged 880 mm (Nobel, 1988).

Table 6. *Annual above-ground dry-weight productivities of CAM plants with high productivities*

Species	Location	Productivity $(\text{Mg ha}^{-1} \text{ yr}^{-1})$	Reference
Agave mapisaga	Mexico, Mexico	25	García-Moya & Nobel (1990)
A. salmiana	Mexico, Mexico	26	García-Moya & Nobel (1990)
A. tequilana	Jalisco, Mexico	25	Nobel & Valenzuela (1987)
Ananas comosus	Hawaii, USA	35	Bartholomew & Kadzimin (1977)
Opuntia ficus-indica	Pernambuco, Brazil; Mexico, Mexico; Texas, USA	18–20	Griffiths (1915); Monjauze & Le Houérou (1965); Flores Valdez & Aguirre Rivera (1979)

Table 7. *Annual above-ground dry-weight productivities of special CAM plantings*

Species	Location	Productivity $(\text{Mg ha}^{-1} \text{ yr}^{-1})$	Reference
Agave mapisaga	Tequexquinahuac, Mexico, Mexico	38	Nobel *et al.* (1992)
A. salmiana	Tequexquinahuac	42	Nobel *et al.* (1992)
Opuntia amyclea	Saltillo, Coahuila, Mexico	45	Nobel *et al.* (1992)
O. ficus-indica	Saltillo	47	Nobel *et al.* (1992)
	Santiago, Chile	47	García de Cortázar & Nobel (1991)

The CAM plants were chosen because of proven high productivities and already had a nearly optimal LAI (the two agaves) or were planted at a spacing leading to a nearly optimal SAI (the platyopuntias); the species in Saltillo were pruned every three months to maintain an optimal SAI. The platyopuntias were all irrigated frequently, and those in Saltillo were also provided with nutrients by means of drip irrigation.

4. Special CAM plantings

Because of the demonstrated high productivity of certain CAM species, field tests have recently been undertaken using computer simulations for the predictions of EPI to define shoot area indices that should be optimal for productivity of CAM plants (García de Cortázar & Nobel, 1991; P. S. Nobel, E. García-Moya & E. Quero, unpublished). In particular, LAI and SAI were generally 4–5 (see Fig. 4). The regions chosen were prime agricultural land, and in addition certain species were irrigated and fertilized (Table 7). For the four species, annual productivity averaged 43 Mg ha^{-1} yr^{-1}. Maximal productivity of 47 Mg ha^{-1} yr^{-1} was achieved by *Opuntia ficus-indica*, both in Chile and in Mexico (Table 7). Such values measured upon harvesting of plant material are consistent with predictions based on EPI. For instance, simulations indicate a maximal productivity of 36 Mg ha^{-1} yr^{-1} for *O. ficus-indica* when the water index was 0·79 in central Chile (Fig. 4); for frequent irrigation, the water index becomes 1·00, so the predicted maximal productivity would then be 36/0·79 or 46 Mg ha^{-1} yr^{-1}, in excellent agreement with the measured value of 47 Mg ha^{-1} yr^{-1} under year-round irrigation (Table 7).

VI. CONCLUSIONS

How do the measured maximal annual above-ground productivities compare with the predictions based on maximal net CO_2 uptake rates? Also, do the energetic arguments for CO_2 fixation by the three photosynthetic pathways make any sense with respect to observed relative maximal productivity? First of all, 50 Mg ha^{-1} yr^{-1} seems to approximate the maximal annual above-ground dry-weight productivity of plants. Of the 22 most highly producing species considered (Tables 5

and 7), only two species had a higher productivity. The second question is more difficult to answer because the comparisons of productivity were not made simultaneously under the same conditions. The six C_3 tree species occurred in regions where winter temperatures probably were limiting for net CO_2 uptake. On the other hand, rigorous selection and breeding efforts to enhance productivity have hardly been attempted for CAM species, in contrast to the situation for C_3 and C_4 agronomic plants, where steady improvement in productivity has occurred throughout the twentieth century (Loomis & Gerakis, 1975; Loomis, 1983; Beadle *et al.*, 1985). Based on the mean maximal annual productivities of the 4–6 most highly producing species in each case, CAM plants had a 12 % lower productivity than the C_4 plants, a 23 % higher productivity than the C_3 agronomic crops, and 10 % higher productivity than the C_3 trees (Tables 5 and 7). This is consistent with the energetic costs of net CO_2 fixation for the three pathways, including the effects of photorespiration, where CAM plants were predicted to be 10 % less efficient than C_4 plants and 15 % more efficient than C_3 plants.

Are there special attributes associated with CAM species of high productivity or should high productivity be universal among CAM plants? The thousands of epiphytic CAM species in the Bromeliaceae, Orchidaceae, and other families would not be expected to have high productivities (Winter *et al.*, 1983; Winter, 1985; Smith *et al.*, 1986). First of all, their growth habit generally precludes a substantial LAI over large areas. Secondly, many are adapted to shaded habitats and so could not effectively utilize a high PPFD. Thirdly, their leaves are relatively thin, especially compared with the massive leaves of *Agave mapisaga* and *A. salmiana* (Tables 6, 7) that average several centimetres in thickness. Thus, the maximal net CO_2 uptake per unit leaf area, which depends on the thickness of tissue available for overnight storage of organic acids, is relatively small for epiphytic CAM species.

Characteristics possessed by highly productive CAM plants include substantial shoot succulence leading to appreciable water storage, central vacuoles in which malate can be stored overnight (in chlorenchyma cells) that are large in volume relative to the cytosol, the ability to synthesize sufficient glucan during the daytime to be able to provide the PEP needed at night (Fig. 2), high levels of PEP carboxylase and tonoplast ATPase at night and of Rubisco during the daytime, a cuticle and epidermis relatively transparent to PPFD, a minimum of opaque spines or other surface coverings, and shallow root systems that are advantageous for water uptake in regions of low rainfall (Ellenberg, 1981; Gibson & Nobel, 1986; Hunt & Nobel, 1987; Nobel, 1988). Environmental factors associated with high productivity of CAM plants are: night-time temperatures near 15 °C, at least for many potentially highly productive species (Kluge & Ting, 1978; Nobel, 1988); a high ambient PPFD, meaning a lack of extensive cloudiness and equatorial or mid-latitude regions; rainfall or irrigation so that the plants can take up water from the soil during most of the year, although shoot succulence and CAM can greatly extend the periods of substantial net CO_2 uptake compared with the situation for C_3 and C_4 species; and absence of prolonged periods of freezing temperatures, especially for agronomically important CAM species. The influence of environmental factors on net CO_2 uptake and productivity can be usefully quantified using EPI, particularly when the effects of soil elements are also included.

Because the high potential productivity of certain CAM plants is only now becoming recognized, increased cultivation of such species can be expected in the future, especially in low latitude regions where water is a major limiting factor for plant productivity. Already *Opuntia ficus-indica* and other platyopuntias are cultivated in over 20 countries in southern Europe, northern and southern Africa, southern North America, and throughout South America for fruits harvested for human consumption, young cladodes used on a limited scale as a vegetable, and mature cladodes used for animal forage and fodder (Russell & Felker, 1987; Nobel, 1988). Agaves are cultivated on three continents for fibre and for the production of alcoholic beverages (Gentry, 1982; Nobel, 1988). Because of the water-conserving nature of CAM, certain lands suitable for CAM species are only marginal for most C_3 and C_4 species, so changes in agricultural practices to increase cultivation of CAM species need not displace current crops. Also, breeding efforts may enhance the productivity and food value of various agaves and cacti. In any case, annual biomass productivities of certain CAM plants can be substantial, exceeding those of most C_3 and C_4 plants, especially in regions with water limitations and when care is taken to optimize shoot area indices.

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