Climate Change and Global Crop Productivity

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14 Crop Ecosystem Responses to Climatic Change: Crassulacean Acid Metabolism Crops

PARK S. NOBEL

Department of Biology, University of California, Los Angeles CA 90095-1606, USA

14.1 Introduction and Background

The best known Crassulacean acid metabolism (CAM) crop species is the bromeliad pineapple (*Ananas comosus*), which is cultivated for its fruit on 720,000 ha in about 40 countries (Table 14.1; Bartholomew and Rohrbach, 1993). However, another CAM species (*Opuntia ficus-indica*), referred to as prickly pear, prickly pear cactus, cactus pear and nopal, is cultivated on just over 1 Mha in about 30 countries (Table 14.1; Russell and Felker, 1987; Nobel, 1996a; Mizrahi *et al.*, 1997). Most such cultivation is for its stem segments (termed cladodes) that are used both for forage and fodder for cattle, goats and sheep; for example, about 400,000 ha are so utilized in Brazil. Cladodes are also harvested as a vegetable for human consumption, especially in Mexico. About 10% of the area for cultivation of *O. ficus-indica* and closely related opuntias is for their fruit, which has long been an important crop in Sicily and is cultivated most extensively in Mexico. About 20 other species in six genera of cacti are also cultivated for their fruits. These include species of *Stenocereus* and other columnar cacti in Mexico (Pimienta-Barrios and Nobel, 1994; Nobel, 1999) and *Hylocereus* and *Seleniocereus* in Colombia, Israel, Mexico, USA, Vietnam, and other countries (Gibson and Nobel, 1986; Mizrahi *et al.*, 1997). This market is relatively small (Table 14.1) but expanding rapidly.

In the early part of this century in various countries in eastern Africa, in substantial areas in India, and in the Americas, another CAM species, *Agave sisalana*, was extensively cultivated for the fibre in its leaves (Gentry, 1982). *Agave fourcroydes* was also cultivated in Mexico, mostly in the Yucatan peninsula. Because of the advent of synthetic fibres that were cheaper and more tolerant of moisture, the cultivation of these two agave species has declined substantially. However, its cultivation is still appreciable (Table 14.1) and certain related species are being considered as new fibre crops (McLaughlin, 1993; Ravetta and McLaughlin, 1996).

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Table 14.1. Principal cultivated CAM species, with part harvested and worldwide cultivation area indicated. Data involve extrapolations and estimates.

Species	Harvested part or purpose	Area of cultivation (ha)	References
Agave fourcroydes, A. sisalana	Leaf fibre	400,000	Gentry, 1982; FAO FAOSTAT Statistics Database (http://apps.fao.org/)
Agave mapisaga, A. salmiana, A. tequilana, various other agaves	Beverages, some fodder	88,000	Gentry, 1982; Nobel, 1994
Ananas comosus	Fruit	720,000	Bartholomew and Rohrbach, 1993; FAO FAOSTAT Statistics Database
Hylocereus, Seleniocereus and *Stenocereus* species, various other cacti	Fruit	14,000	Mizrahi *et al.*, 1997; Pimienta-Barrios and Nobel, 1994
Opuntia ficus-indica, other opuntias	Fodder, forage, vegetable	900,000	Barbera *et al.*, 1995; Nobel, 1994
	Fruit	95,000	
	Cochineal dye, chemicals	50,000	
Total		2,267,000	

Other agaves are currently cultivated for alcoholic beverages, especially *Agave tequilana* for tequila. In addition, about ten species of agave are cultivated for mescal (also spelled mezcal), which, like tequila, is a distilled beverage, and for pulque, a fermented beverage. Commercial production of all these occurs in Mexico.

The present worldwide cultivation of agaves as crops totals nearly 500,000 h (Table 14.1). To this number which can be added those agaves used as ornamental plants or for fences and erosion control. In addition to agaves, many species of cacti are also so utilized for these purposes. Because none of these CAM crops is particularly tolerant of freezing temperatures, nearly all cultivation of agaves, cacti and pineapple occurs within 30° latitude of the Equator (Nobel, 1988; Bartholomew and Rohrbach, 1993; Bartholomew and Malézieux, 1994). If temperatures rise as predicted during global climatic change, the regions suitable for the cultivation of such CAM plants will expand (Nobel, 1996b).

The most convincing evidence indicating that agaves, cacti and pineapple are CAM plants is the substantial nocturnal CO_2 uptake by their photosynthetic organs, which occurs in all three groups (Joshi *et al.*, 1965; Neales, 1973; Sale and Neales, 1980; Nose *et al.*, 1986; Nobel, 1988; Borland and Griffiths, 1989; Medina *et al.*, 1991). Because photosynthesis cannot occur without light, the CO_2 taken up at night cannot be immediately fixed into photosynthetic

products such as glucose and sucrose. Rather, the CO_2 is incorporated into phosphoenolpyruvate (PEP) by the enzyme PEP carboxylase, leading to the formation of an organic acid such as malate. Nocturnal acidification of the chlorenchyma can be easily tested to demonstrate CAM in various species, including agaves, cacti and pineapple (Neales, 1973; Friend and Lydon, 1979; Nobel, 1988; Medina *et al.*, 1991, 1993). A sophisticated but indirect method for determining whether or not a particular species uses CAM is to find the ratio of various carbon isotopes in the plant tissues. In particular, differences in the enzymes involved in the initial fixation of carbon and the subsequent biochemical processing of the fixed carbon lead to unique isotopic signatures for the three photosynthetic pathways: CAM (which is the only photosynthetic type with nocturnal stomatal opening), C_3 and C_4. Thus, isotopic analysis of carbon by mass spectroscopy of tissue samples can indicate the photosynthetic pathway. This has been done for all three groups of CAM crops (agaves, cacti and pineapple) and all exhibit CAM (Nobel, 1988; Medina *et al.*, 1994).

A relevant question with respect to global climatic change and its influences on productivity (the major theme of this book) is what is the effect of increasing atmospheric CO_2 concentrations ($[CO_2]$) on net CO_2 uptake by CAM plants? Another question about CAM plants concerns effects on their gas exchange and productivity caused by changes in other environmental factors, such as air temperature, photosynthetic photon flux (PPF, wavelengths of 400–700 nm that are absorbed by photosynthetic pigments) and soil water status (quantified by the soil water potential and reflecting the effects of rainfall). Environmental effects on net CO_2 uptake and biomass productivity among CAM plants have been studied most extensively for *O. ficus-indica*, but sufficient data exist for predictions for other commercial CAM species as well.

One way to quantify the effects of environmental factors on net CO_2 uptake is to use an environmental productivity index (EPI; Nobel, 1984, 1988, 1991b). The individual environmental factors affect net CO_2 uptake multiplicatively, not additively. For instance, if prolonged drought causes daily stomatal opening to cease, then no net CO_2 uptake will occur, regardless of whether or not light levels and temperatures are optimal for CO_2 uptake. EPI can be represented as follows:

$$\text{EPI} = \text{fraction of maximal daily net } CO_2 \text{ uptake} \qquad \text{(Eqn. 14.1)}$$

$$= \text{water index} \times \text{temperature index} \times \text{PPF index}$$

The water index, which like the other indices ranges from 0 when it is totally limiting for daily net CO_2 uptake to 1 when it does not limit CO_2 uptake, represents the fractional limitation due to soil water availability; hence, it progressively decreases during drought. The temperature index quantifies the limitations of temperature on daily net CO_2 uptake, and the PPF index quantifies the effects of light. Because CAM plants take up CO_2 primarily at night, the photosynthetic responses represented by the PPF index relate total daily net CO_2 uptake over 24 h periods (mol CO_2 m^{-2} per day) to the total daily PPF (mol photons m^{-2} day^{-1}). All the indices in equation 14.1 are determined over 24 h periods.

A fourth multiplicative index can be incorporated into equation 14.1 to quantify the effects of nutrients on daily net CO_2 uptake. Such a nutrient index has been determined for various species of agaves and cacti, for which five elements (N, P, K, B and Na) have major influences on daily net CO_2 uptake (Nobel, 1989). For plants maintained under various ambient CO_2 levels for prolonged periods (months), the effects of $[CO_2]$ are most readily incorporated into predictions of net CO_2 uptake by making measurements over 24 h under conditions of wet soil, optimal temperatures and saturating PPF. Increases in $[CO_2]$ can also affect the influences of other environmental factors on net CO_2 uptake by CAM plants.

14.2 Gas Exchange

Crops with C_3 and C_4 type photosynthesis, which are the principal focus of this book and currently represent over 98% of cultivated crops in terms of land area utilized, inherently have a much lower water-use efficiency (WUE) than CAM plants. The WUE equals the net CO_2 fixed by photosynthesis divided by the water lost via transpiration on an instantaneous, daily or seasonal basis. The water vapourcontent of saturated air, which accounts for virtually all the air spaces within shoots of plants, increases essentially exponentially with temperature. For example, air saturated with water vapourcontains 6.8 g of water vapour m^{-3} at 5°C, 17.3 g m^{-3} at 20°C, and 39.7 g m^{-3} at 35°C. The water vapour content of the air surrounding plants is generally far below the saturation value and does not change much during the course of a day unless a major change in weather occurs. For air containing 4.0 g of water vapour m^{-3} (relative humidity of 59% at 5°C, 23% at 20°C, and 10% at 35°C), the shoot-to-air difference in water vapour content is 2.8 g m^{-3}, 13.3 g m^{-3}, and 35.7 g m^{-3} at the respective temperatures. The rate of water loss depends on this shoot-to-air difference in water vapourcontent and the amount of stomatal opening; for the same amount of stomatal opening, transpiration is thus 13.3/2.8 or 4.8-fold higher at 20°C than at 5°C and 35.7/13.3 or 2.7-fold higher at 35°C than at 20°C. If the shoot and air temperatures are 15°C cooler during the night than during the day (which is realistic where CAM plants are grown) transpiration would be three to five times lower during the night than during the day for the same amount of stomatal opening. This underscores the importance of nocturnal stomatal opening for water conservation by CAM plants. CAM crops also tend to have a lower maximal stomatal conductance than do C_3 and C_4 crops, which further reduces water loss (Nobel, 1988, 1994).

Plants using the C_3 or the C_4 photosynthetic pathway have a net CO_2 uptake only during the day, whereas CAM plants take up CO_2 predominantly during the night. However, they can also take up CO_2 during the day, especially when soil water is not limiting (Fig. 14.1). Any evaluation of shoot gas exchange over 24 h periods, as is necessary and conventional for CAM plants (Fig. 14.1), automatically includes the contribution of respiration to net CO_2 uptake. The maximal instantaneous rates of net CO_2 uptake by *Agave mapisaga* and *O. ficus-indica* occur at night and can be greater than those

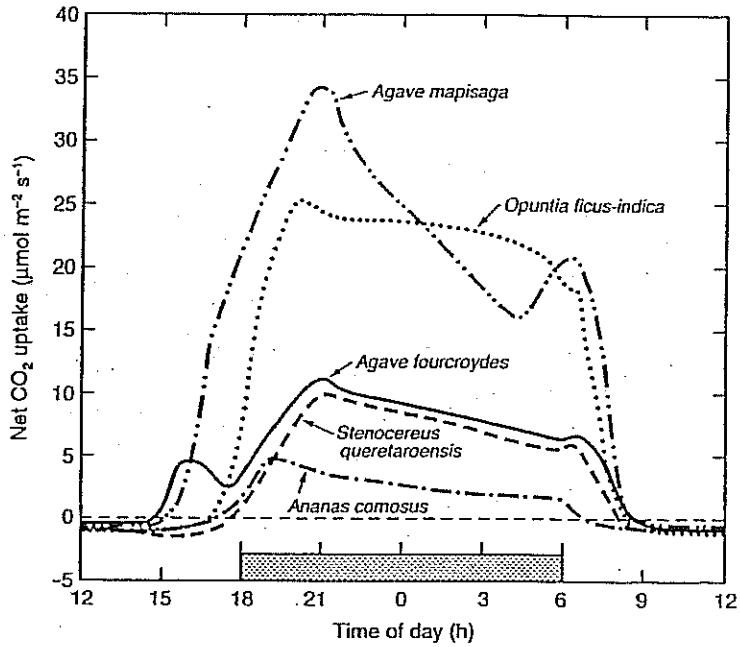

Fig. 14.1. Net CO_2 uptake over 24 h period for various cultivated CAM species under approximately optimal conditions. Data for leaves of *Agave mapisaga* are from Nobel *et al.* (1992); for leaves of *Agave fourcroydes* from Nobel (1985); for leaves of *Ananas comosus* at a suboptimal PPF averaging 360 µmol m^{-2} s^{-1} from Medina *et al.* (1991); for stems of *Opuntia ficus-indica* from Nobel (1988) and P.S. Nobel (unpublished observations); and for stems of *Stenocereus queretaroensis* from Nobel and Pimienta-Barrios (1995) and P. S. Nobel (unpublished observations).

of most other perennials whose maximal rates occur during the day. The instantaneous net CO_2 uptake rates of these highly productive CAM species can exceed 25 µmol m^{-2} s^{-1} (Fig. 14.1), whereas nearly all ferns, shrubs and trees, as well as many C_3 and C_4 crops, have lower maximal uptake rates (Nobel, 1991b). The maximal net CO_2 uptake rates for *A. fourcroydes* and *Stenocereus queretaroensis* are about 10 µmol m^{-2} s^{-1} lower and are similar to those of many other perennials. Maximum instantaneous values for net CO_2 uptake by *Ananas comosus* examined over 24 h periods by various research groups are relatively low (Bartholomew and Malézieux, 1994); for example, 2.2 µmol m^{-2} s^{-1} (Borland and Griffiths, 1989), 2.4 µmol m^{-2} s^{-1} (Nose *et al.*, 1986), 3.6 µmol m^{-2} s^{-1} (Neales *et al.*, 1980) and 4.9 µmol m^{-2} s^{-1} with a suboptimal PPF (Fig. 14.1; Medina *et al.*, 1991). Indeed, net CO_2 uptake by *A. comosus* has apparently not been measured under optimal conditions. Yet because of the high WUE of all of these CAM species, they can have a relatively high productivity when cultivated under dryland (non-irrigated) conditions. In the future, the most important and relevant comparisons among crops differing in photosynthetic pathway may be based on WUE, because the

available supply of groundwater is steadily decreasing, as is the supply of uncontaminated surface water available for irrigation at a reasonable cost.

14.3 Values for Component Indices of Environmental Productivity Index

To determine the component indices of EPI (equation 14.1), plants are generally placed in environmental chambers, and one environmental factor is varied while the others are maintained at optimal values. Net CO_2 uptake is then measured over 24 h periods. The only commercial CAM species for which the environmental indices relating to soil water status, temperature and PPF (equation 14.1) have been fully determined are *A. fourcroydes*, *O. ficus-indica* and *S. queretaroensis*; partial results are available for *Ananas comosus* (Neales *et al.*, 1980; Sale and Neales, 1980; Nose *et al.*, 1986) and *Agave salmiana* (Nobel *et al.*, 1996). Thus, these are the species whose net CO_2 uptake over 24 h periods can most readily be predicted in response to the environmental changes accompanying global climatic change. Extrapolations to other CAM species can be made if differences among the examined species can be rationalized.

At about 9 days of drought for *A. fourcroydes* and 13 days for *A. salmiana* the water index decreases 50% from its value of 1 under wet conditions (Fig. 14.2). The water index decreases more slowly for the stems of these two cacti used as crops because they have a much greater volume of tissue water storage per unit area across which water can be transpired. Drought of 23 days for *O. ficus-indica* and 36 days for *S. queretaroensis* reduces the water index by 50% (Fig. 14.2) The volume available for water storage per unit surface area (which indicates the average tissue depth supplying water for transpiration) is about 4 mm for leaves of *A. fourcroydes* (Nobel, 1985), 8 mm for leaves of *A. salmiana* (Nobel *et al.*, 1996), 22 mm for the stems of *O. ficus-indica* (Nobel, 1988) and 78 mm for stems of *S. queretaroensis* (Nobel and Pimienta-Barrios, 1995). A water index based on nocturnal acid accumulation (an indirect indication of total daily net CO_2 uptake) decreases 50% in 12 days for *A. salmiana*, which has an average water storage depth of 7 mm in its leaves (Nobel and Meyer, 1985), and in 7 days for *A. tequilana*, which has an average water storage depth of 3 mm in its leaves (Nobel and Valenzuela, 1987). For these five species, an empirical relation of 4.8 times the square root of the tissue depth for water storage (in millimetres) accurately predicts the drought duration in days that will cause the daily net CO_2 uptake to be halved. Unfortunately, the response of the Water Index to drought has not been studied for *Ananas comosus* (Bartholomew and Malézieux, 1994).

The optimal temperatures for net CO_2 uptake by the five cultivated CAM species presented in Fig. 14.3 fall within the range found for other CAM species (Nobel, 1988), but the temperatures are lower than for nearly all other cultivated crops. In particular, most net CO_2 uptake for commercial CAM species occurs at night; consequently, nocturnal temperatures are more important than are diurnal ones with respect to total daily net CO_2 uptake.

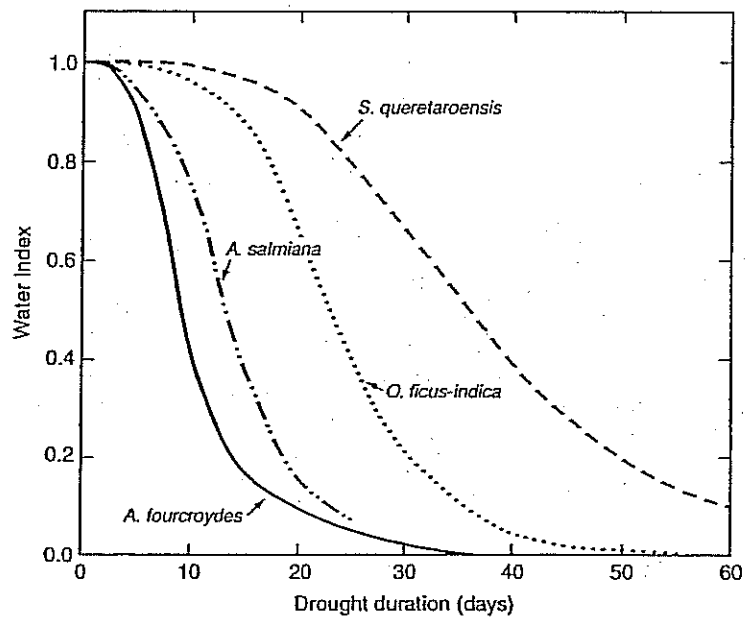

Fig. 14.2. Responses of the water index (see equation 14.1) to drought duration for *Agave fourcroydes, A. salmiana, O. ficus-indica,* and *S. queretaroensis.* Drought refers to the period when the shoot has a lower water potential than the soil just outside the roots in the centre of the root zone. Data for *A. fourcroydes* are from Nobel (1985); for *A. salmiana* from Nobel *et al.* (1996); for *O. ficus-indica* from Nobel and Hartsock (1983, 1984); and for *S. queretaroensis* from Nobel and Pimienta-Barrios (1995) and P.S. Nobel (unpublished observations).

Maximal daily net CO_2 uptake occurs at night-time temperatures of about 18°C for *A. fourcroydes*, 13°C for *A. salmiana*, 15°C for *Ananas comosus*, 15°C for *O. ficus-indica*, and 16°C for *S. queretaroensis* (Fig. 14.3). The optimal temperature for nocturnal net CO_2 uptake is about 15°C for *Agave americana* (Neales, 1973), and the optimal temperatures for nocturnal acid accumulation are about 12°C for *A. salmiana* (Nobel and Meyer, 1985; Nobel *et al.*, 1996) and 15°C for *A. tequilana* (Nobel and Valenzuela, 1987). Thus the optimal night temperature for daily net CO_2 uptake is about 15°C for all of these cultivated CAM species. This is a major consideration when determining where CAM plants will be cultivated. Temperature cannot be easily manipulated in the field, other than by location of the cultivated plots, whereas the water status can be controlled by irrigation and by light interception through spacing of plants, which affects interplant shading.

The responses of daily net CO_2 uptake to PPF are remarkably similar for the commercial CAM species examined, with 50% of maximal uptake occurring at a total daily PPF of 10 mol m^{-2} per day for *A. fourcroydes*, *Ananas comosus* and *S. queretaroensis* and at 11 mol m^{-2} day^{-1} for *O. ficus-indica* (Fig. 14.4). Moreover, the total daily PPF at which total daily net CO_2 uptake was zero was about 2 mol m^{-2} day^{-1} for all four species, with 95% of the

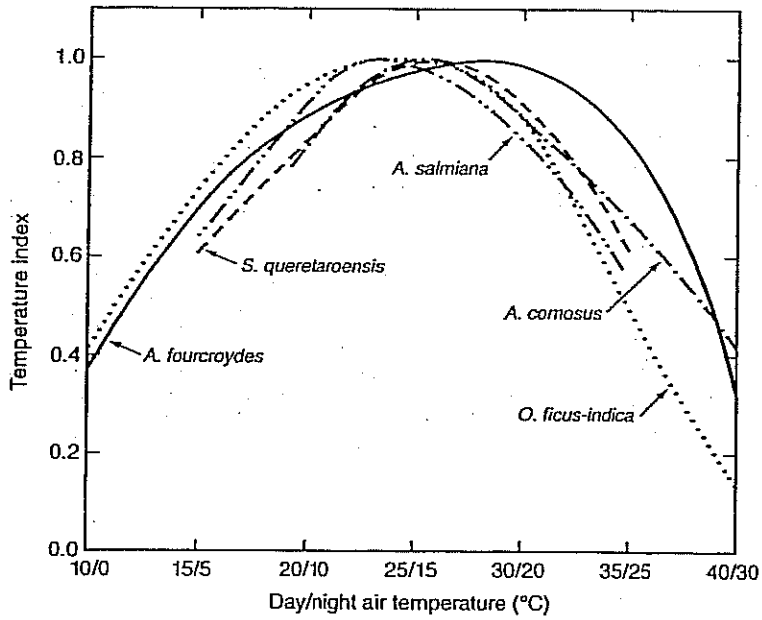

Fig. 14.3. Responses of the temperature index (see equation 14.1) to day/night air temperatures for *Agave fourcroydes, A. salmiana, Ananas comosus, O. ficus-indica* and *S. queretaroensis*. The plants were routinely kept at a particular day/night temperature regime for 10 days to allow for acclimation (Nobel, 1988). Data are for mean night temperatures for *S. queretaroensis* and for constant night temperatures for the other species. They are from the references cited in Fig. 14.2, plus Connelly (1972), Neales *et al.* (1980) and Bartholomew and Malézieux (1994) for *Ananas comosus*.

maximal net CO_2 uptake being achieved at a total daily PPF of about 25 mol m^{-2} day^{-1} (Fig. 14.4). Half of maximal nocturnal acid accumulation occured at a total daily PPF of 9 mol m^{-2} per day for *A. salmiana* (Nobel and Meyer, 1985) and at 11 mol m^{-2} day^{-1} for *A. tequilana* (Nobel and Valenzuela, 1987); therefore the PPF responses of such cultivated CAM species are nearly identical. In this regard, the chlorenchyma for all of the agave and cactus species is a relatively thick 3–5 mm, and the amount of chlorophyll per unit surface area is a relatively high 0.7–0.9 g m^{-2} (Nobel, 1988). Thus, the light-absorbing properties of the photosynthetic organs are similar, leading to their similar responses of net CO_2 uptake to incident PPF as quantified by the PPF index (Fig. 14.4).

As mentioned above, a nutrient index can also be incorporated as a multiplicative factor in equation 14.1, although relatively little information on nutrient responses of CAM crops is available. Based on studies with four agave species and eleven cactus species, most of which are not crops, the five soil elements having the greatest effect on net CO_2 uptake, growth and biomass productivity are N, P, K, B and Na (Nobel, 1989); other macronutrients and micronutrients will likely have important effects as well and may be

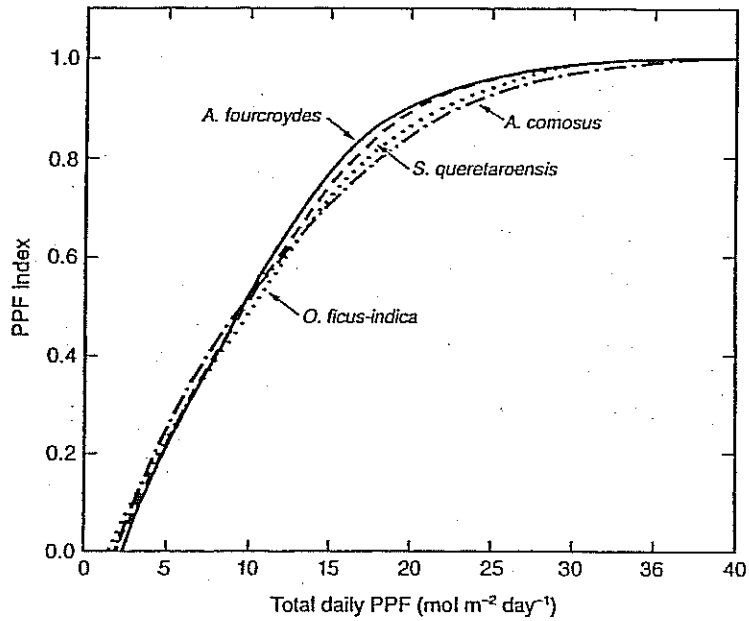

Fig. 14.4. Responses of the PPF Index (see equation 14.1) to the total daily PPF for *Agave fourcroydes, Ananas comosus, O. ficus-indica,* and *S. queretaroensis.* Data for the agave and the cacti are for the PPF in the planes of the photosynthetic surfaces and are from the references cited in Fig. 14.2. For pineapple, data are for the PPF in a horizontal plane incident on the canopy and are from Sale and Neales (1980) and Nose *et al.* (1986).

particularly limiting in certain soils. Growth and biomass productivity are optimal at about 3 mg N g^{-1} (0.3% by soil mass), 60 μg P g^{-1} 250 μg K g^{-1} and 1.0 μg B g^{-1} (Nobel, 1989). Suboptimal levels leading to half the maximal values are about 0.7 mg N g^{-1}, 5 μg P g^{-1}, 3 μg K g^{-1} and 0.04 μg B g^{-1}.

Soil Na inhibits biomass productivity for the agaves and cacti tested with 20% inhibition occurring at about 60 μg Na g^{-1} and 50% inhibition occurring at about 150 μg Na g^{-1} (Nobel, 1989). The decrease in growth resulting from increasing soil salinity is apparently less for *Ananas comosus* than for agaves and cacti, but little quantitative data are available (Bartholomew and Malézieux, 1994). In this regard, salinity can increase in arid and semi-arid regions as a consequence of poor land management practices and even global climatic change (Schlesinger *et al.*, 1990; Vitousek, 1994).

14.4 Productivity

Most productivity studies on agronomic C_3 and C_4 species were done before 1975 (Loomis and Gerakis, 1975). After that time, the focus has been on increasing their harvest index (fraction of the plant harvested), as well

as on aspects of plant performance that can be affected by molecular biology/biotechnology. Very little such attention has been devoted to CAM plants, although efforts to preserve the germplasm with field plantings in various countries have been made with prospects for increased productivity and future biotechnology in mind. CAM plants in nature are generally relatively slow-growing, but productivity for certain cultivated CAM species can be high. For example, the dry weight productivity of two cultivated CAM species, *Opuntia amyclea* and *O. ficus-indica*, equals or exceeds the highest

Table 14.2. Maximal net CO_2 uptake and productivity of cultivated CAM plants, with comparisons for the C_3 and C_4 species with the highest productivities.

Species	Maximal net CO_2 uptake rate ($\mu mol\ m^{-2}\ s^{-1}$)	Maximal daily net CO_2 uptake ($mmol\ m^{-2}\ d^{-1}$)	Maximal productivity (t dry weight $ha^{-1}\ year^{-1}$)	References
Agave fourcroydes, A. sisalana, A. tequilana	11	360–400	about 15	Nobel, 1985; Nobel and Valenzuela, 1987; Nobel, 1988
Agave mapisaga, A. salmiana	29–34	1050–1170	38–42	Nobel *et al.*, 1992
Ananas comosus	5	240–310	20–31	Bartholomew and Kadzimin, 1977; Bartholomew, 1982; Bartholomew and Rohrbach, 1993; Medina *et al.*, 1991; Zhu *et al.*, 1997a
Opuntia amyclea, O. ficus-indica	26–28	940	45–50	Nobel *et al.*, 1992; Garcia de Cortázar and Nobel, 1992
Stenocereus queretaroensis	10	320	—	Nobel and Pimienta-Barrios, 1995
Six highest C_3 crops	av. 39	av. about 900	29–45	Loomis and Gerakis, 1975; Loomis, 1983; Nobel, 1991a
Six highest C_3 trees	–	–	36–44	Jarvis and Leverenz, 1983; Nobel, 1991a
Six highest C_4 crops	av. 46	av. about 1200	32–70	Loomis and Gerakis, 1975; Loomis, 1983; Nobel, 1991a

values for all C_3 crops and trees and is exceeded by only a few C_4 crops (Table 14.2; Nobel, 1991a, 1996a). Moreover, because of the water-conserving characteristics of CAM (high WUE), the productivity of CAM plants can be substantially higher than that of C_3 and C_4 plants under conditions of low availability of soil water, an increasingly important aspect for crops worldwide.

Productivity per unit ground area per year, which is crucial for assessing agronomic potential, can be related to the net CO_2 uptake characteristics of plants (Nobel, 1988). In this regard, *A. mapisaga, A. salmiana, O. amyclea,* and *O. ficus-indica* have the highest maximal net CO_2 uptake rates among CAM crops, averaging 29 $\mu mol\ m^{-2}\ s^{-1}$, which is only 30% less than the average reported maximal rates for the C_3 and C_4 crops with the highest rates (Table 14.2). Net CO_2 uptake for CAM plants is generally measured and expressed for the surface most exposed to the incident PPF (one side of a leaf or a stem, which is usually opaque). For the thin leaves of C_3 and C_4 plants, net CO_2 uptake is measured for both sides of a leaf but is expressed per unit area of one side (the projected leaf area). If net CO_2 uptake by the sides of leaves or stems of CAM plants facing away from the highest PPF is also included, then the maximal rates are actually rather similar among plants of the three photosynthetic pathways. Because net CO_2 uptake by CAM plants can occur during both day and night (Fig. 14.1), compared with C_3 and C_4 plants which have net CO_2 uptake only during the day, the maximal daily net CO_2 uptake for these four highly productive CAM species is intermediate between the six C_3 crops with the highest values and the equivalent six C_4 species, even though a different area basis is conventionally used (Table 14.2). Moreover, for the CAM crops, the maximal total daily net CO_2 uptake is highly correlated with the maximal instantaneous net CO_2 uptake rate. Plant productivity per unit ground area for the various CAM crop plants considered is also highly correlated with the total daily net CO_2 uptake per unit photosynthetic surface area, although the actual productivity in the field depends on interplant spacing.

CAM plants minimize the energetically expensive release of CO_2 via photorespiration by presenting high levels of CO_2 to the pivotal enzyme, ribulose-1,5-bisphosphate carboxylase-oxygenase (Rubisco) (Nobel, 1988, 1991a, 1994). Thus photorespiration is relatively low for CAM plants, as is also the case for C_4 plants. Based on energy costs for the production of ATP and NADPH and the number of these molecules required for the fixation of CO_2 into carbohydrates, the total cost per carbon molecule fixed for CAM species is lower than that for C_3 species and only slightly higher than that for C_4 species (Nobel, 1991a, 1996a). Thus the intermediate values of total daily net CO_2 uptake and of long-term productivity by highly productive CAM species compared with similar C_3 and C_4 crops (Table 14.2) can be explained at a cellular level. This increases confidence in predictions that certain CAM crops will be more extensively cultivated in the future (Nobel, 1994, 1996a,b; Mizrahi *et al.*, 1997), because the CAM pathway can lead to high productivity.

14.5 Effects of Elevated [CO_2]

Although the long-term effects of months of elevated [CO_2] on net CO_2 uptake and productivity are relatively unstudied for commercial CAM species, such effects must be evaluated in view of the global climatic change caused by the just over 2 μmol CO_2 mol^{-1} current annual increase in [CO_2] (Houghton *et al.*, 1990; King *et al.*, 1992; Vitousek, 1994). In this regard, *Ananas comosus* growing for 4 months at 730 μmol CO_2 mol^{-1} has 23% more dry mass than plants growing at 330 μmol mol^{-1} (Zhu *et al.*, 1997b). Its nocturnal increase in leaf acidity is 42% higher for the approximately doubled [CO_2]. Studies using $\delta^{13}C$ indicate that most of the enhancement in net CO_2 uptake for *Ananas comosus* under elevated [CO_2] is at night via the CAM pathway, rather than during the day via the C_3 pathway (Zhu *et al.*, 1997b). Apparently the only species of agaves whose long-term responses to elevated [CO_2] have been studied are *A. deserti*, which is a CAM species but not a cultivated one, and *A. salmiana*. Raising the [CO_2] from 370 to 750 μmol mol^{-1} increases daily net CO_2 uptake by 49% throughout a 17-month period for *A. deserti* (Graham and Nobel, 1996). More leaves are produced per plant under the doubled [CO_2]. The combination of increased total leaf surface area and increased net CO_2 uptake per unit leaf area enhances dry mass accumulation by *A. deserti* under the doubled [CO_2] by 88% (Graham and Nobel, 1996). *Agave salmiana* grown for 4.5 months at 730 μmol CO_2 mol^{-1} has 55% more new leaves, 52% more fresh mass and a 59% higher net CO_2 uptake rate than when grown at 370 μmol mol^{-1} (Nobel *et al.*, 1996). Another experiment with *A. salmiana* and *S. queretaroensis* maintained at 720 μmol CO_2 mol^{-1} for 1 month led to a 36% higher net CO_2 uptake for both species when compared with plants grown with 360 μmol mol^{-1} (Nobel, 1996b).

Most research on the effects of elevated [CO_2] on a cultivated CAM species has been done with *O. ficus-indica*, and ranges from studies focusing on enzymes (Israel and Nobel, 1994; Nobel *et al.*, 1996; Wang and Nobel, 1996) to those focusing on productivity (Nobel, 1991c; Cui *et al.*, 1993; Nobel and Israel, 1994). Responses of plants to elevated [CO_2] depends on other factors besides CO_2, with one of the most important being soil volume (Arp, 1991; Thomas and Strain, 1991; Berntson *et al.*, 1993). When soil volume per plant is low, responses of net CO_2 uptake to a doubling of the [CO_2] are minimal, as is also the case for *O. ficus-indica* maintained in pots for 4 months (Nobel *et al.*, 1994). For *O. ficus-indica* in the field for 5 months, daily net CO_2 uptake is 35% higher at 520 μmol mol^{-1} and 49% higher at 720 μmol mol^{-1} than at 370 μmol mol^{-1}. Production of dry mass is 21% and 55% higher, respectively, at the two elevated [CO_2] levels compared with the current ambient one (Cui *et al.*, 1993). Such effects are maintained after canopy closure and for a total of 15 months; biomass productivity is then 47 t dry weight ha^{-1} $year^{-1}$ at 370 μmol CO_2 mol^{-1} and 65 t ha^{-1} $year^{-1}$ at 720 μmol mol^{-1} (Nobel and Israel, 1994). The responses of daily net CO_2 uptake by *O. ficus-indica* to other environmental factors have also been checked at the doubled [CO_2]. In particular, raising [CO_2] increases the percentage enhancement of net CO_2 uptake by increases during drought as temperature is raised and PPF is lowered (Nobel and Israel,

1994). Consequently, EPI (equation 14.1) can be adjusted to reflect different responses of net CO_2 uptake to environmental factors as [CO_2] increases in the future. To summarize the results for all of the cultivated CAM species examined for months under elevated [CO_2], daily net CO_2 uptake and biomass productivity increases about 1% for each increase of 10 μmol mol^{-1} in atmospheric [CO_2].

14.6 Conclusions and Future Research Directions

Environmental influences on net CO_2 uptake and, ultimately, productivity are predictable for the CAM species that are cultivated commercially, especially agaves and cacti. Such CAM plants do not tolerate freezing temperatures well–injury occurs at –5°C for most species (Nobel, 1988) – and so cultivation is limited to low latitudes. Increases in latitudinal ranges for such species are expected to accompany future global warming (Nobel, 1996b). Net CO_2 uptake is maximal at night air temperatures near 15°C, whereas day temperatures are relatively unimportant, as stomates of commercially important CAM crops tend to be closed then. Because of similar chlorenchyma characteristics among species, the PPF responses are similar, with 50% of maximal net CO_2 uptake occurring at a modest total daily PPF of 10 mol m^{-2} d incident on the photosynthetic surface. Such responses cause net CO_2 uptake per unit ground area to be maximal at a leaf or stem area index (total surface area basis) per unit ground area of about four (Nobel, 1991a). Decreases in availability of soil water during drought cause net CO_2 uptake by such cultivated CAM plants to rely on water stored in the shoot. The average water storage depth in the transpiring organs of CAM plants directly indicates the drought duration that can be tolerated while still maintaining substantial rates of net CO_2 uptake. The responses to elevated [CO_2] are also rather similar among the CAM crops considered and amount to a 1% increase in daily net CO_2 uptake, and hence productivity, per 10 μmol mol^{-1} increase in [CO_2] (Nobel, 1996b).

Future research will inevitably be devoted to biotechnological improvements in the yield and general performance of cultivated CAM species. Because agaves and cacti are currently important crops in Mexico and other mainly Latin American countries, information transfer from these to other regions where they can be cultivated profitably will be important (Nobel, 1994). This will also entail changes in cultural practices as new fruits, vegetables and beverages become available and new sources of forage and fodder are used for domesticated animals. The increased [CO_2] accompanying global climatic change will be advantageous for net CO_2 uptake and productivity by CAM crops. The accompanying increased temperatures will favour cultivation at higher latitudes and a somewhat lower daily net CO_2 uptake during the warmer part of the year in the hotter regions presently used for cultivation. The effects of changes in other environmental factors accompanying global climatic change (such as seasonal rainfall patterns and cloudiness) on net CO_2 uptake and productivity can also be predicted (equation 14.1). The high

productivity of certain cultivated CAM species under optimal conditions (Table 14.2) and the generally high WUE of CAM plants under all conditions warrants increased agronomic exploitation of such plants in the future. These plants can be expected to have generally favourable or, in any case, predictable responses of daily net CO_2 uptake to the forecasted environmental changes.

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