Photosynthesis and Photorespiration-

II. C_4 Plants: Advantages and Paradoxes

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Abstract

After a brief description of the main characteristics of C_3 plants, a review on the main features of C_4 plants with benefits such as improved photosynthetic performance under high temperature and strong light, better water and nitrogen use efficiency was considered essential to discuss. The advantages of C_4 plants are mainly the result of a system combining a CO_2 pump and an anatomical specialization of differentiated cells in the leaves. These theoretical benefits were compared with results of agronomy and eco-physiological analysis to reveal the paradoxical correlation between water use efficiency (WUE) and a lower resistance to severe water limitations and a low dominance in hot and arid sunny regions for non-grass plant species. The main differences between the C_3 and C_4 photosynthetic systems are illustrated by unidirectional exchanges of oxygen. In contrast to C_3 plants, the low level of photorespiration results in a low O_2 uptake and a lack of complementary variation in reactions of carboxylation and oxygenation. This 'mirror effect' illustrates the role of a 'sink' for photochemical energy that might indicate a recognized positive role of photorespiration during water limitation, and probably during variations of bright light. This absence may cause the paradox stated above. An evolutionary analysis of the kinetics of Rubisco, the enzyme that fix CO_2, shows that Rubisco of C_4 plants can be considered relatively poorly advanced with a low ratio (*V*o:*V*c) of the maximum rate of oxygenation (*V*o) to carboxylation (*V*c). This ratio is considered to be a factor that characterizes, in higher plants, the protective role of photorespiration.

1. Introduction

The primary production of biomass of the planet is based on Rubisco enzyme that fixes CO_2 through its function as a carboxylase. The path of atmospheric CO_2 at the site of the enzyme varies among different plant types. This difference facilitates a well-known classification among plant types as C_3, C_4 and CAM plants (Edwards and Walker, 1983). The C_3 plants use the simplest way between the atmosphere and the chloroplasts, which are the organelles that contain both chlorophyll and Rubisco systems. In fact, this enzyme catalyzes both reactions with CO_2 and oxygen as substrates. Two antagonistic processes, i.e. carboxylation and oxygenation, are responsible for two antagonistic phenomena, i.e. photosynthesis (adding one carbon) and photorespiration (removing one carbon) to/from the substrate RuBP, respectively (Tolbert, 1971; Peterhansel et al., 2010).

Abbreviations

P=Net CO_2 uptake or net O_2 evolution; *PR*=Photorespiration; *U*=gross oxygen uptake; *E*=gross O_2 evolution; *ETR*=Electron transport rate in chloroplasts; *ETR*/4=*E*; CAM=Crassulacean acid metabolism; PEP=Phosphoenolpyruvate; NAD-ME, PCK, NADP-ME=Sub-pathway types of C_4 plants (NAD-malate enzyme, PEP-carboxykinase, and NADP-malate enzyme, respectively); *WUE*=Water use efficiency; *NUE*=Nitrogen use efficiency; PNUE=Photosynthetic nitrogen use efficiency; RuBP=Ribulose-1,5-bisphosphate; τ=Specificity factor for CO_2 of Rubisco; *K*c, *K*o=respectively Michaelis constants for carboxylation and oxygenation of Rubisco; *V*o, *V*c=Maximum, and *vo*, *vc*=Current rates of oxygenase and carboxylase of Rubisco, respectively.

Photorespiration significantly reduces photosynthesis in C_3 plants, not only through decarboxylation but also via differ ent oxidases associated with it. Thus, the primary yield of photosynthesis was reduced by over 50% in C_3 plants in the pre-industrial era (Gerbaud and André, 1979; André, 2011ac). C_4-type plants, that are the subject of this paper, have developed various mechanisms for increasing the concentration of CO_2 in the vicinity of Rubisco to reduce and virtually eliminate photorespiration. Despite this advantage, they represent only about 3% of terrestrial plant species. However, in some areas, they represent a much higher percentage of photosynthetic organisms by biomass.

1.1. The characteristics of C_3 plants

The characteristics of C_3 plants have been analyzed by direct measurements of carboxylase and oxygenase reactions obtained by the isotope labelling of $^{18}O_2$ gas exchanges (André, 2011c). The responses of photosynthesis and photorespiration in response to changes in atmospheric CO_2 or O_2 have the following characteristics (Gerbaud and André, 1979, 1980; Canvin et al., 1980; Badger, 1985; André, 2011ab).

1.1.1. Mirror effect

There is an antagonistic and complementary variation of P and U. For low and middle order irradiance (100-800 μ mole photon m^{-2} s^{-1}) this variation is symmetrical. The photochemical energy created in the chloroplasts, measured by the gross oxygen evolution (E), is constant and its use is divided according to local pressures of CO_2 and O_2. This produces curves similar to mirror images, the importance of which was emphasized by André (2011abc).

1.1.2. Strong light and variable CO_2

In strong light (1200-1800 μ mole photon m^{-2} s^{-1}) and variable CO_2, E is not constant and increases with the pressure of CO_2 (Canvin et al., 1980 (figure 3, page 304); Badger, 1985 (figure 2, page 37). Since CO_2 assimilation is either RuBP or Rubisco limited (von Caemmerer, 2000), the E value declines with low CO_2 pressure. This implicates a regulation of the electron transport chain, because the production of energy, potentially equal to P_{max}, exceeds the biochemical use. This situation can create constraints and photoinhibition (André, 2011bc). However, the sharing of E between P and U follow the rule of a mirror effect if E normalizes the exchanges.

1.1.3. Influence of conductance (g) on transport of CO_2: sink effect of oxygenation

Conductance of the diffusion and the transport of CO_2 play a major role in the ratio CO_2:O_2, and therefore the P:PR ratio. The mirror effect is used to simulate the variation of this ratio. For example, during stomata closure under water stress conditions, which is common in natural ecosystems as well as in agro-ecosystems, and in sunny mid-day period often coupled with atmospheric saturation water vapour deficits. One can thus view the role of PR as 'sinks' that can (or cannot) absorb and dissipate the excess energy (ETR) produced in chloroplasts. This ability is a function of Vo:Vc, i.e. the ratio of maximum rates of oxygenation and carboxylation of Rubisco. This factor is termed oxygenation capacity (OC) (André, 1986, 2011b). The sink effect has been observed in many experiments (André, 2011b).

1.1.4. Role of PR in response to variable bright lights

An analysis of the responses of P and U at different lights and increasing pressure of CO_2 shows a linear relationship between the sum ($P+U=E$) and illumination, irrespective of the CO_2 level. Based on the assumptions of Farquhar et al. (1980) and assuming that the Mehler reaction is negligible:

$$P=vc-0.5vo-R \tag{1}$$

$$U=vo+0.5vo+R \tag{2}$$

$$E=P+U=vc+vo \tag{3}$$

R is the 'dark-mitochondrial' respiration partially maintained in the light, whereas vo and vc denote current velocity of oxygenase and carboxylase of Rubisco.

It has been noted that there is sharing of electron flow used by U and P according to a same mirror effect when exchanges are normalized by E. Moreover, for any level of CO_2 (Canvin et al., 1980) $E=P+U=vc+vo$ (equation 3) varies linearly with the irradiance. However, $vc+vo$ is the turnover of RuBP. It is not saturated or limited contrary to the assumptions of the model of Farquhar et al. (1980) and its applications especially in von Caemmerer (2000) (figure 3.11, page 86). There is simply a sharing of the chemical energy produced in the chloroplasts between photosynthesis and photorespiration pathways. That second mirror effect could be very useful as regulation of the alternating low and high light, for example in sun flecks (André, 2011ac).

2. C_4 Plants

Pioneering research on anatomical, biochemical and physiological features and mechanisms of C_4 plants have been reviewed by Hatch (2002) and El-Sharkawy (2009). The readers are further directed to reviews by Ehleringer et al. (1991) and Sage (2001, 2004) for information on the evolution and characteristics of C_4 plants.

2.1. Short history of C_4 plants

C_4 plants have been important since the past human civilization. The Mesoamerican civilization was based on maize and the grain amaranth cultivation (NRC-BOSTID, 1984, 1989), and the trans-Atlantic slave trade was based on sugarcane plantations. More recently, the expansion of grasslands and crops at the expense of the forest, with their consequent effect on global climatic change, is worrying. The C_4 system appeared later than the C_3 system, approximately 24-35 million years ago.

However, the greatest differentiation occurred between 5 and 8 million years ago and this, independently occurred in many families comprising grasses (Ehleringer et al., 1991). Nevertheless, C_4 plants remain a minority: only about 7,500 species, in contrast to about 30,000 CAM and 2,50,000 C_3 species. More important is the fact that they are mainly herbaceous and not ligneous plants, barring a few exceptions such as *Chamaesyce olowaluana* in Hawaii (Sage, 2004). Is this due to their later evolution? This will be the subject of this work to propose additional explanations.

2.2. Differences from C_3 plants

C_3 and C_4 plants mainly differ in the carboxylation processes and the anatomy of leaves (Slack and Hatch, 1967; Laetsch, 1974; Edwards et al., 2001). As you will recall, the photosynthesis processes of C_4 plants are divided between mesophyll and bundle sheath cells, i.e. Kranz anatomy (a term first coined by G. Haberlandt, 1914). A difference in assimilate products was first made by Karpilov (1960) in maize. C_4 syndrome, in a dicot plant (*Amaranthus*) as well as in several tropical grasses, was about the first finding linking Kranz anatomy and photosynthetic characteristics by El-Sharkawy and Hesketh (1965). Later in sugarcane, Kortschak et al. (1965), and Hatch and Slack (1966) observed that the first carboxylation processes concerned molecules with four carbon atoms and not three, like that in the C_3 carbon cycle (Calvin and Bassham, 1962). Both carbon pathways were discovered with $^{14}CO_2$ labelling.

Two steps of the C_4 photosynthesis that occur in the mesophyll cells are the light-dependent reactions and a preliminary fixation of CO_2 into a molecule called malate or aspartate. CO_2 is released from malate or aspartate in the bundle sheath cells, where Rubisco and the Calvin-Benson cycle fix it again. The PEP produced is then recycled back to the mesophyll cells, and subsequently the carbohydrate products of photosynthesis are distributed through the plant (Slack and Hatch, 1967).

Apart from the flowering plants, the C_4 carboxylation process has also been found in some algae. Hence, the Kranz anatomy is most likely not essential for the photosynthesis of all terrestrial C_4 plants, as was observed in some species of Chenopodiaceae where a functional C_4 cycle occurs in a single cell (Voznesenskaya et al., 2001; Sage, 2002).

It is interesting to note that C_4 systems were added to the pre-existing C_3 system, where the last one is generally maintained in cells of C_4 plants. This is the case during the development of maize seedlings (Veau and Burris, 1989; Kutschera et al., 2010). The existence of C_3-C_4 intermediate photosynthesis like Cassava (*Manihot esculenta* Crantz) with high photosynthetic rate and several C_4 like characteristics (low *PR*, low CO_2 compensation point, presence of PEPC and of C_4 assimilates) reveals a step of C_4 plants in evolution and stimulates further research on crop improvement (El-Sharkawy, 1993, 2004) (see below). Differences were observed between C_4 plants having different enzymes and sites for decarboxylating C_4 dicarboxylic acids in bundle sheath cells (Aubry et al., 2011). Phenomena of CO_2 leakage out of bundle sheath cells with higher conductance is greater in NAD-ME and PCK sub-pathway types than in NADP-ME and greater in dicots than in monocots (Kiirats et al., 2002; Kubasek et al., 2007; Kromdijk et al., 2008). This could be linked to residual photorespiration and could explain the difference of resistance to water stress (Ellis et al., 1980; André, 2011b). Comparative ecophysiology with C_3 plants was established (Pearcy and Ehleringer, 1984) and is discussed below.

2.3. O_2 and CO_2 exchange in C_4 plants

Measurement of unidirectional oxygen exchange was made by Volk and Jackson (1972) in maize using $^{18}O_2$ labelling. A very low rate of O_2 uptake was observed indicating low photorespiration. Similar results were obtained by André and Gerbaud (1979). However, the photorespiration pathway remains active, as demonstrated by Veau and Burris (1989) comparing $^{18}O_2$ labelled compounds in wheat and maize. The most interesting data were obtained by Canvin et al. (1980) and Badger (1985), with the response curves of O_2 exchanges versus CO_2 concentrations being depicted in figure 1.

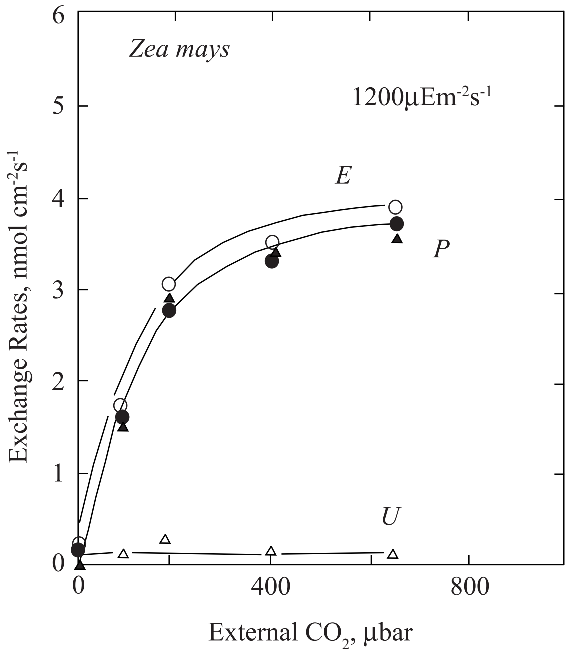

Figure 1: Effect of CO_2 on O_2 and CO_2 assimilation in maize (*Zea mays*) at light intensity of 1200 µ mol photons m^{-2} s^{-1} and 28°C leaf temperature. O, gross O_2 evolution (*E*); Δ, O_2 uptake (*U*); ●, net O_2 evolution (P); ▲, net CO_2 uptake (*P*). (To compare with figure 1, in André, 2011c). Reprinted with permission from Badger (1985); copyright Annual Review of Plant Physiology, (Ed.)

The main result is illustrated in figure 1, with the following characteristics, in contrast with figure 1 in André, 2011bc):

a) a very small O_2 uptake, independent of CO_2 levels.
b) a very low CO_2 compensation point, both indicating quasi suppression of *PR*.
c) a non-symmetrical variations of *P* and *U*, i.e. the total absence of a mirror effect
d) a decline in gross O_2 evolution (*E*) with the decrease in CO_2 concentration.
e) O_2 uptake is independent of the CO_2 or O_2 pressure (last data not shown).

The most important difference from the pattern of gas exchanges of C_3 plants (Gerbaud and André, 1979, 1980; Canvin et al, 1980; Badger, 1985; André, 2011abc) is the very low O_2 uptake and consequently the total absence of a mirror effect, and thus of the oxygenation capacity. The importance of the last parameter was highlighted (André, 1986, 2011c) and discussed below.

Consequent to (a, d & e), the crossing point, i.e. values of CO_2 and O_2 concentrations for which O_2 uptake equals CO_2 uptake (André, 2011a) is practically at the CO_2 compensation point. There is no reduction of photosynthesis if O_2 increases. The equilibrium of CO_2 and also O_2 require the effect of feedbacks and the crossing points play an important role in the plant-atmosphere biosystem (André, 2011a).

2.4. Theoretical advantages of C_4 plants

C_4 plants are generally considered to possess the most evolved photosynthetic system (Sage, 2004). However, the analysis of their ecophysiological distribution in the planet shows that the advantages only concern specific environments and mainly grasses. The advantages can be summarized as follows (El-Sharkawy, 2009):

- High optimum temperature, related to the effect of temperature on the τ of Rubisco, which increase the *PR* in C_3 plants.
- Lower mesophyll resistance to CO_2 diffusion, coupled with higher stomatal resistance, hence higher leaf *WUE.*
- Existence of the so-called Kranz anatomy and the higher degree of exposed mesophyll surface area cell^{-1} volume.
- The ability to recycle respiratory and photorespiratory CO_2 by illuminated leaves.
- A better photosynthetic nitrogen use efficiency (PNUE), i.e. the amount of carbon fixed unit^{-1} leaf nitrogen (Sage et al., 1987).

Most of these advantages are due to the increased CO_2 concentration near the final enzyme of carboxylation, i.e. Rubisco. It increases the resulting *plant* CO_2 affinity (André, 2011a) and reduces or practically suppresses the photorespiration. The density of veins in leaves, already observed in C_3 plants as a positive photosynthetic factor, also contributes to the photosynthetic performance.

2.4.1. Quantum yield for CO_2 uptake

Ehleringer and Bjorkman (1977) compared two groups of seven C_3 and five C_4 plants from ecologically diverse habitats. The quantum yield of photosynthesis was calculated from the absorbed light (mol CO_2/absorbed mol photon) in a common atmosphere of 21% O_2 and 325 ppm CO_2. At 30°C, there was no notable difference between C_3 (0.0524±0.0014) and C_4 (0.0534±0.0009). Under 2% O_2, the quantum yield of C_4 remained unchanged (0.0538±0.0011), but the yield of C_3 plants increased to 0.0733±0.0008. Therefore, the cost of *PR* in C_3 plants may be equal to the cost of pre-fixation of CO_2 in C_4 plants via PEPC.

A similar study (Ehleringer and Pearcy, 1983) confirmed this data with the addition of a separate analysis of dicots and grasses, with a better yield of C_4 grasses above 20°C. The differences between the sub families of C_4 grasses reveal a little benefit of NADP-ME and PCK in comparison to NAD-ME.

Results of yield studies are in accordance with Da Matta et al. (2001), who compared current and potential photosynthesis of nine C_3 and five C_4 crop plants. While the actual assimilation rates, on leaf area basis, under ambient CO_2 and temperature varied, the potential of assimilation under saturating light, high CO_2, and optimal temperature (35°C) was very similar. This finding corroborates the earlier report by El-Sharkawy and Hesketh (1965) where both C_3 and C_4 plants had similar photosynthetic rates at 1,000 ppm external CO_2, intense light and optimal temperature.

2.4.2. Temperature effect

With a variation in temperature, the yield of C_4 was constant but the yield of C_3 plants decreased above 30°C and increased below that value. The changes in the quantum yields of C_3 plants are due to changes in the O_2 inhibition by the photorespiration.

The conclusion is the C_4 syndrome gives an advantage only in particular environments. For example, in absence of *PR* (2% O_2), C_3 plants have an advantage. The great advantage of C_4 plants is the independence of yield from temperature, which provides an edge under conditions of high temperature.

Conversely, in temperate regions, low light intensity is a prominent disadvantage for C_4 plants. These conditions, on the other hand, provide an advantage for C_3 plants due to their lower rate of photorespiration and because they need no energy for the primary fixation of CO_2 that exists in C_4 system.

2.4.3. Crop yield

However, these data at single leaf level is in contrast with the common finding that C_4 plants have a better photosynthesis and thereby a greater potential to increase crop productivity. The figure of 50% better growth rate is proposed (Hibberd et al., 2008; Aubry et al., 2011).

The comparisons of crop yields were controversial. Inconsistent conclusions concerning the relative productivity of C_3 and C_4 have been drawn, where authors, such as Gifford (1974) compared plant species growing in diverse environments. They observed the large potential advantage of the C_4 mechanism at the biochemical level is progressively attenuated in moving from the microscopic to the macroscopic parameters until, at the level of crop growth rate, there is no apparent difference between best examples of the two groups when grown in their own preferred natural environments. Loomis and Gerakis (1975) concluded that C_4 species were more productive at low latitudes but less productive at high latitudes. This is coherent with the ecophysiology (Ehleringer et al., 1991, 1997) and was confirmed by an analysis conducted later (Snaydon, 1991). However, Liu and Osborne (2008) demonstrated that there is no inherent barrier to the development of cold acclimation in C_4 species in grasses of the Mongolian eco-system.

One energetic cost of the C_4 pathway is the leakiness of bundle sheath tissues, whereby a variable proportion of the CO_2 concentrated in bundle sheath cells diffuses back to the mesophyll. Based on studies of carbon isotopic discrimination measuring the rate of leakage, Kromdijk et al. (2008) identified the leakage as an important limitation to CO_2 uptake of crops with the C_4 pathway; at the canopy level the reduction in canopy CO_2 uptake was estimated to be 14%. This effect was attributed to an incomplete inhibition of photorespiration, especially under high light, and an increase in the relative contribution of mitochondrial respiration at low light (Kromdijk et al., 2010).

Besides being photosynthetically superior, the crop performances of C_4 plants like maize are also enhanced due to the breeding selection of hybrids endowed with the heterosis effect. Likewise, the effect of an efficient canopy is probably important in sugarcane yields.

2.4.4. *Water use efficiency (WUE)*

The strategy of C_4 plants and the CO_2 pump system allow for the same internal pressure of CO_2 to have a lower stomata opening, and therefore less transpiration. This process increases the instantaneous leaf water use efficiency (CO_2 uptake/H_2O loss) as well as the *WUE* at the crop level (total biomass/water used) (Briggs and Shantz, 1914; Boyer, 1996). Likewise, the population analysis of C_3 and C_4 plants in natural environments reveals a paradox to be considered and discussed further.

2.4.5. *Nitrogen use efficiency (NUE)*

At equal photosynthesis, C_3 plants invest more nitrogen in their leaves, mostly in Rubisco, than C_4 plants, in spite of the weak performance of their Rubisco (Sage et al., 1987). However, since organic nitrogen is remobilized to fill out the seeds, this does not seem a decisive advantage to C_4 plants.

2.5. *Ecophysiology of C_4 plants*

The ecophysiology of C_4 plants has been reviewed earlier (Pearcy and Ehleringer, 1984; Ehleringer et al., 1997; Taub, 2000) with the general tendency of an adaptation in warm to hot open sites. It is agreed that the primary selective factor influencing the evolution of C_4 photosynthesis was changes in atmospheric CO_2 concentration (low level in the past) rather than aridity or high temperatures (Ehleringer et al., 1991, 1997). Osborne and Freckleton (2009) analyzed the habitat data for 117 genera of C_3 and C_4 grasses, representing 15 lineages. They have shown that C_4 grasses occupy a wider range of drier habitats than their C_3 counterparts, including mesic, arid and saline habitats. But it is important to note that it concerns mainly grasses as discussed below.

2.6. *Competition C_3-C_4*

The previous results (section 2.5) typically concern grasses. Baskin and Baskin (1978) re-examined the hypothesis that C_4 plants are better competitors than C_3 plants, and that most weeds in summer crops have C_4 photosynthesis. With reference to the eastern United States, it is concluded that both C_3 and C_4 weeds are poor competitors, many noxious weeds of cultivated crops have C_3 photosynthesis, and in general C_4 photosynthesis is less important than other features of plants in determining their growth rate and competitive ability.

C_4 plants have substantial acclimation potential, but in most cases lag behind the acclimation responses in C_3 plants. For example, some C_4 species are unable to maintain high quantum yields when grown in low-light conditions. Others fail to reduce carboxylase content in shade, leaving substantial over-capacity of Rubisco and PEP carboxylase in place (Sage and McKown, 2005). These authors (Sage and McKown, 2005) also observed that shade-tolerant C_4 grasses lack the capacity for maintaining a high state of photosynthetic induction following sun flecks, and thus may be poorly suited to exploit subsequent sun flecks compared to C_3 species. This reinforces the role of photorespiration as a sink for energy in case of high light regulation evoked above (section 1.1.4) and analyzed in André (2011ac).

Overall, the evidence indicates that C_4 photosynthesis is less phenotypically plastic than C_3 photosynthesis, and this may contribute to the more restricted ecological and geographical distribution of C_4 plants across the Earth (Sage and McKown, 2005).

Thus, the presence of the C_4 pathway alone was not sufficient to yield a competitive advantage over the C_3 species under water-limited conditions (Pearcy et al., 1981; Ehleringer et al., 1997).

Even in desert plant communities, C_4 species do not appear to be competitively superior to C_3 species as discussed below.

2.7. C_4 paradox- C_4 versus C_3 in arid environments or dry seasons

It was shown that in both North American (Teeri, 1977; Taub, 2000) and Namibian deserts (Ellis et al., 1980), most of the grasses were C_4 plants. Nevertheless, these authors were dubious about the resistance of C_4 plants, noting that the C_3 type predominates in the non-grass component of the flora of the central Namibia desert. We add, after Syvertsen et al. (1976), that in the Chihuahuan Desert of Mexico the C_4 plants (grasses) predominate in less dry areas (90% of biomass); however, they practically disappear in the driest areas, representing 2% of the biomass versus 48% for CAM and 50% for C_3 types. Hence, C_3 plants are found in all ecosystems, from tundra to deserts, and are amongst the major plants in the deserts of Egypt, Arabia, Iraq and India, according to the survey of Ziegler et al. (1981), who showed that 87% of dicots and 69% of all these plants were C_3 plants. Edwards and Still (2008) investigated the relative influences of phylogeny and photosynthetic pathway in determining the ecological distribution of C_4 grasses in Hawaii. They revealed that the restriction of C_4 grasses to warmer areas is largely due to their evolutionary history as members of a warm-climate grass clade, but that the C_4 pathway does appear to confer a competitive advantage to grasses in more arid environments.

Ripley et al. (2007) investigated the paradox of the correlation between the decline of C_4 species in arid environments despite their high *WUE*. They studied two sub-types, C_4 and C_3 plants of *Alloteropsis semialata*, and they concluded that a decline in the electron transport chain activity, and thus a lower photochemical efficiency in both types. In contrast to the C_4 type, there was a relative increase in the electron transport to alternative sinks in the C_3 type, in particular to *PR*, during a fall in carbon reduction. Such results are in good agreement with the stress experiments using $^{18}O_2$ data described in André (2011b). Further investigations (Ripley et al., 2010) showed that within the Panicoid grasses, C_4 (NADP-ME) species are more sensitive to drought than C_3 species and recover more slowly from drought. This was also observed by Ellis et al. (1980) and Ehleringer et al. (1997) and a hypothesis of a difference in oxygenation capacity was proposed (André, 2011b).

2.8. O_2 exchange and stress resistance- usefulness of photorespiration

The role of photorespiration as an undesirable phenomenon is well accepted. However, from an evolutionary point of view, photorespiration cannot be trashed as undesirable, owing to its association with such a huge metabolism (more than 50% of photochemical energy was spent for it at the beginning of the industrial era) (Gerbaud and André, 1979; André, 2011a). The hypothesis of its significance by a protective effect was proposed by Osmond (1981) and explained by an evolution in Rubisco (André, 1986, 2011b) and also by the co-evolution plant-atmosphere (André, 2011a).

The significance is now more widely recognized, not only by its sink energy properties under stress conditions (Wingler et al., 2000; Peterhansel et al., 2010) but also by exporting reduced components from chloroplasts to the mitochondrion (Igamberdiev and Lea, 2002). Its necessary contribution to the atmospheric O_2/CO_2 equilibrium is noted by Igamberdiev and Lea (2006) and has been analysed by André (2011a).

The review of Reumanna and Weber (2006) highlights recent developments in understanding photorespiration and identifies gaps in the knowledge of this important metabolic function. Therefore, the competitive advantage conferred by C_4 metabolism will be progressively reduced with the increase of CO_2 concentration (Sage, 2004).

2.9. Rubisco properties and evolution

2.9.1. Previous knowledge

A review by Yeoh et al. (1981) demonstrated a large difference of *K*c between terrestrial C_3 and C_4 plants, about two times lower in C_3 ones (12-25 to 28-34 µ molar, respectively), indicating a better CO_2 affinity of Rubisco in C_3 plants. Rubisco from aquatic angiosperms, fresh water or marine algae has consistently yielded high *K*c values similar in range to that of the enzyme from C_4 terrestrial plants. The differences were precisely measured by Jordan and Ogren (1981) with a more complete knowledge of the specificity factors τ and their different components *K*c, *K*o and *V*o:*V*c. The specificity factor of Rubisco was only improved by two times from cyanobacteria to modern C_3 or C_4 plants. The only significant difference between C_3 and C_4 plants was about the *K*c.

2.9.2. A re-examination

Evolutionary problems concerning Rubisco and the difference between algae, C_4 and C_3 plants were re-examined by André (1986, 2011b). The main result of that review is illustrated in figure 2.

According the Laing et al. (1974) equations:

$$vc/vo = (Vc/Vo)\,(Ko/Kc)\,CO_2/O_2 \qquad (4)$$

Then, for a given O_2 concentration, the rate of the carboxylase varies like:

$$vc \approx Vc.1/Kc.\ CO_2 \text{ (if } Vo \text{ and } Ko \text{ are constant)} \qquad (5)$$

figure 2 shows the following:

- According to Jordan and Ogren (1981) that *Evolutionary pressures seem to have directed the enzyme towards more efficient utilisation of CO_2* the Rubisco evolution can be plotted along the scale in the increase of the CO_2 affinity (1/*Kc*), i.e. the rate of the carboxylase (equation 5).
- Considering maize as a representative of C_4 plants, the

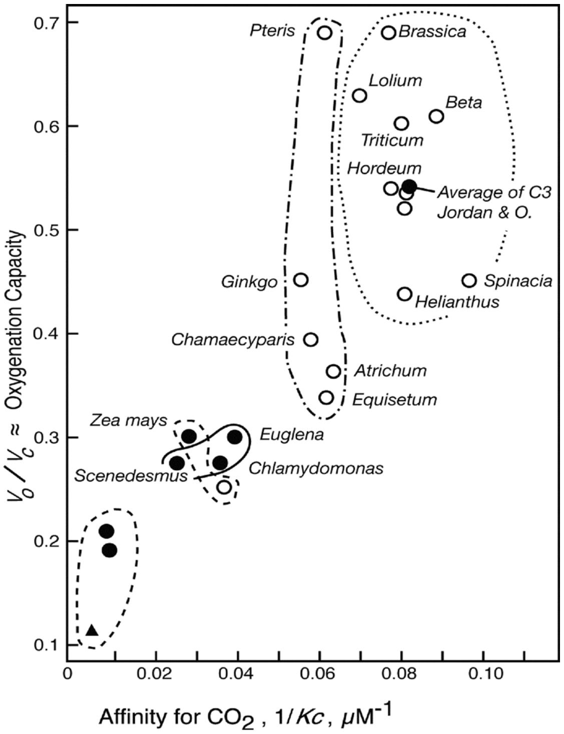

Figure 2: Species variation of the ratio of maximum velocities of oxygenase to carboxylase of Rubisco as an index of oxygenation capacity (the ability of oxygenation to replace carboxylation in the case of CO_2 limitation, i.e. the mirror effect)
Data: (●) Jordan and Ogren (1981); (○) Bird et al. (1982); and (σ) Andrew and Abel (1981). From the last two sources *V*o:*V*c was calculated from *K*c and *K*o assuming, after Jordan and Ogren (1981, 1983), that the specificity factor was constant in terrestrial C_3 plants and assumed an average of 80
(---) cyanobacteria; (—) green algae; (----) *Z. mays*; (- . - . -) lower plants; and (......) higher plants
(from André, 2011b, by courtesy of BioSystems, Elsevier Eds.)

1/*Kc* of Rubisco of the C_4 plants is three times lower than the 1/*Kc* of higher C_3 plants, in accordance to Yeoh et al. (1981).

- The Rubisco of C_4 plants is similar to that of algae, also in accordance to Yeoh et al. (1981). It could be considered as *relatively* primitive or less evolved or following a regressive way.
- The general trends of figure 2 show that the progress in CO_2 affinity is accompanied by the increase in the ratio *V*o:*V*c. According to the equation (4), this trend shows that the oxygenase is also relatively increased by up to five times, relative to that of carboxylase. This has been explained (André, 1986, 2011b) by the increase of the oxygenation capacity, in other words, by the increase of the symmetrical relationship (mirror effect) between O_2 uptake (*U*) and CO_2 uptake (*P*), the two main consumers of reductive equivalents produced in chloroplasts. (c.f. equation 1, 2, 3, and figure 1 in André, 2011c).

2.10. Genetic engineering

An obvious target for genetic engineering is to reduce photorespiration, mainly by the improvement of the Rubisco specificity factor (Long, 1998; Long et al., 2006; Loomis and Amthor, 1999; Parry et al., 2003; Yu et al., 2005). The results are disappointing because the specificity factor is the less variable parameter of higher plants evolution (Jordan and Ogren, 1981), but the knowledge of *PR* pathway and its genetic control was increased. To improve the photosynthetic yield by reducing *PR*, new opportunities are expected from inducing a C_4 like CO_2 concentrating mechanism or from the modification of the *PR* pathway by different ways (Hibberd et al., 2008; Häusler et al., 2001; Peterhansel et al., 2010; Peterhansel and Maurino, 2011).

Chen and Ye (2001) have obtained increases of photosynthetic oxygen evolution in chloroplasts or leaves of spinach treated with oxaloacetate (OAA) and malate (MA), suggesting the possibility to improve the photosynthetic efficiency by building up a micro-cyclic system of C_4 dicarboxylic acid in C_3 plants. This was verified by Ji et al. (2004) who proposed that photosynthetic C_4 micro-cycle was promoted in a great range in transgenic rice by the introduction of a maize specific PEPC gene. The enhancement of photosynthetic C_4 micro-cycle further played a role in raising the net photosynthetic rates (*P*) and of photochemical efficiency in comparison to the wild type. In a very important and complex experiment, Kebeish et al. (2007) introduced the *Escherichia coli* glycolate catabolic pathway into *Arabidopsis thaliana* chloroplasts to directly convert glycolate to glycerate and to create a partial shortcut of the *PR* pathway. The photosynthesis and the biomass were increased by up to 40%. Another strategy involves the modification of the structure and function of leaves to reduce the resistance to CO_2 transfer.

These results will provide scientific evidence for genetic breeding to improve photosynthetic efficiency in crops by gene engineering. The way is long from experiments in *A. thaliana* to crop applications but it will be important to know if the reduction in photorespiration provokes the same changes in the model as the ones observed by other ways, like CO_2 enrichments or previous genetic manipulations. Photorespiration contributes to the nitrogen cycle. The suppression of photorespiration strongly inhibits nitrate assimilation. Thus, nitrate assimilation in both dicot and monocot plants depends on photorespiration (Rachmilevitch et al., 2004). Inhibition of photorespiration strongly suppresses nitrate and ammonium assimilation (Bloom et al., 2010). Enrichment of atmospheric CO_2 (FACE experiments) showed that the reduction of photorespiration increased biomass of tree. It was accompanied by an increase of nitrogen uptake in soils (Norby and Iversen, 2006). Luo et al. (2006) analyzed 104 scientific publications and concluded that a concomitant increases in C and N contents in plant and soil pools at elevated CO_2 in response to rising atmospheric CO_2 concentration. This problem remains controversial if we consider the numerous experiments of CO_2 enrichment (FACE) and the conclusion of Taub (2010), who proposed that under elevated CO_2 concentration, most plant species show higher rate of photosynthesis, increased growth, decreased water use and lowered tissue concentrations of nitrogen and protein.

3. Conclusion

3.1. Natural environments

From these data, we could say that the C_4 syndrome, especially the CO_2 pump (and the huge increase of internal CO_2) has compensated the very low quality of Rubisco (figure 2). The dominance of C_4 plants in dry lands, when it exists, mainly concerns grass species. Standing plants are mainly C_3, with rare exceptions. C_4 grasses are well adapted in particular environments (hot and often dry lands) due to a good WUE, a fast growth and a shorter life cycle. Hence, contrary to CAM and standing C_3 plants, C_4 grasses have an 'avoidance strategy' to face water stress. In natural environments, their survival is assumed by seeds or roots. Fires are often associated to their ecological equilibrium: C_4 grasslands and savannas are the most frequently burnt eco-systems in the word (Bond et al., 2005). The indisputable advantage of C_4 plants is to solve the problem of growth under low level of atmospheric CO_2, probably why Ehleringer et al. (1991) suggest that C_4 plants evolved as alternative response to a reduction in atmospheric CO_2 levels that began during the Cretaceous and continued until Miocene. But that situation was not generalized, because as demonstrated by André (2011a), a stable equilibrium of atmosphere in O_2 is problematic if the productive system of biomass and oxygen (plants) is a C_4 like system, without *PR*, i.e. without any O_2 concentration feed back, except fires. Following the same reasoning than Ehleringer et al. (1991), it was proposed (André, 2011ac) that C_3 plants and Rubisco evolved as alternative response to the excess of oxygen producing the paleo fires (Berner, 1999). This is coherent with the association of grasslands and fires in C_4 eco-systems (Bond et al., 2005): that could be the case of a terrestrial system based only on C_4 plants.

3.2. C_4 crop plants

We have seen (section 2.4.1) that the quantum yield of C_4 plants is better only in particular hot environments. Their *WUE* is not a guarantee for a better resistance and of a competitive advantage (section 2.6, 2.7). Following the conclusion of Wingler et al. (2000), a first opinion could be that photorespiration metabolism is not only an wasteful process inevitably resulting from the kinetic properties of Rubisco, but precisely because of this inefficiency, it is also involved in stress protection and alternative high light regulation (section 1.1.4 & 2.6). Furthermore, photorespiration provides metabolites for other metabolic processes, e.g. glycine for the synthesis of glutathione, which is also involved in stress protection. Abolishing photorespiration by engineering Rubisco or *PR* pathway may, therefore, not necessarily lead to improved plant performance, especially under unfavorable growth conditions.

Nevertheless, the best theoretical aim should be to combine Rubisco characteristics of C_3 plants (good oxygenation capacity) with some advantages of algae like the CO_2-concentration mechanism. The results would be to increase the mesophyl conductance of C_3 plants, more important in plant photosynthesis than a good specificity factor of Rubisco (André, 2011ac). This was the strategy studied by Sage and Sage (2009) and obtained in the experiments of Ji et al. (2004). Alternatively, another strategy should be to increase the low performances of the Rubisco in C_4 plants (figure 2) to increase their oxygenation capacity and to contribute to solve the C_4 paradox by using the quality of photorespiration as sink energy and safety process. This could also be the case of C_3-C_4 intermediate plants, like cassava (*Manihot esculenta* Crantz), which possesses an elevated activity of the enzyme PEP carboxylase that may recycle respiratory CO_2. It is a tropical root crop that is highly productive in favorable environments as well as highly tolerant to prolonged droughts (El-Sharkawy, 2004). Similar compromises could be expected by genetic manipulation.

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