ACTUAL AND POTENTIAL PHOTOSYNTHETIC RATES OF TROPICAL CROP SPECIES

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ABSTRACT - The actual (A) and potential (A_{pot}) photosynthetic rates of C_3 and C_4 tropical crop species grown under greenhouse conditions was compared. The following species were investigated: *Oryza sativa, Phaseolus vulgaris, Glycine max, Helianthus annuus, Gossypium hirsutum, Manihot esculenta, Theobroma cacao, Coffea arabica, Hevea brasiliensis*, and *Eucalyptus urophylla × E. grandis*, all from the C_3 group, and *Amaranthus* sp., *Panicum maximum, Pennisetum purpureum, Zea mays* and *Saccharum officinarum*, from the C_4 group. A, determined under non-limiting light at ambient temperature and CO_2, was measured with an infrared gas analyser, whilst A_{pot}, determined under saturating light and CO_2 at an optimal temperature (35 ^{o}C for all species), was gauged with a gas-phase oxygen electrode. On an area basis, A varied from 5.0 up to 26.3 μmol CO_2 m^{-2} s^{-1}, whilst A_{pot} was very similar in 14 of the 15 species, with an average rate of 35.0 ± 2.4 μmol O_2 m^{-2} s^{-1}. The value of A_{pot} in *T. cacao* was approximately half the mean of the remaining species. On a mass basis, variations in A were much larger, and differences in A_{pot}, although not large, emerged. The overall mean A_{pot} per unit mass in the four tree species was 28.0 ± 2.2 μmol O_2 g^{-1} min^{-1} against 44.6 ± 5.8 μmol O_2 g^{-1} min^{-1} in the remaining species. As a whole, the results evidenced a conservative behaviour of the photosynthetic apparatus to fix CO_2 amongst the species investigated, despite the large differences in A among them.

ADDITIONAL INDEX TERMS: Carbon assimilation rate, photosynthetic oxygen evolution, specific leaf area.

TAXAS FOTOSSINTÉTICAS ATUAL E POTENCIAL DE ESPÉCIES TROPICAIS CULTIVADAS

RESUMO – Compararam-se as taxas fotossintéticas atual (A) e potencial (A_{pot}) de espécies tropicais C_3 e C_4 cultivadas sob condições de casa-de-vegetação. Foram estudadas as seguintes espécies: *Oryza sativa, Phaseolus vulgaris, Glycine max, Helianthus annuus, Gossypium hirsutum, Manihot esculenta, Theobroma cacao, Coffea arabica, Hevea brasiliensis*, e *Eucalyptus urophylla × E. grandis*, todas do grupo C_3, e *Amaranthus* sp., *Panicum maximum, Pennisetum purpureum, Zea mays* e *Saccharum officinarum*, do grupo C_4. A, determinada sob alta irradiância e temperatura e CO_2 ambientes, foi medida com um analisador de gases a infravermelho, enquanto A_{pot}, determinada sob luz e CO_2 saturantes e à temperatura ótima (35 ^{o}C para todas as espécies), foi medida com um eletrodo de oxigênio de fase gasosa.

Em base de área, A variou desde 5,0 até 26,3 µmol CO_2 m^{-2} s^{-1}, enquanto A_{pot} foi similar em 14 das 15 espécies avaliadas, com uma taxa média de 35.0 ± 2.4 µmol O_2 m^{-2} s^{-1}. Observou-se um padrão diferencial em *T. cacao*, em que A_{pot} decresceu, aproximadamente, em 50% em relação a A_{pot} das demais espécies estudadas. Em base de massa, as variações em A foram bem maiores e diferenças em A_{pot}, embora não expressivas, puderam ser observadas. Os valores médios de A_{pot} por unidade de massa, nas quatro espécies lenhosas, foi 28.0 ± 2.2 µmol O_2 g^{-1} min^{-1}, contra 44.6 ± 5.8 µmol O_2 g^{-1} min^{-1} nas espécies remanescentes. Como um todo, os resultados evidenciaram um comportamento conservado do aparelho fotossintético, em termos de fixação do CO_2, nas espécies estudadas, a despeito das largas diferenças em A entre elas.

TERMOS ADICIONAIS PARA INDEXAÇÃO: Área foliar específica, evolução do oxigênio fotossintético, taxa de assimilação do carbono.

INTRODUCTION

Large differences in the actual photosynthetic rates (A), termed herein as the maximum net rate of carbon uptake under non-limiting photosynthetic photon flux (PPF) at ambient temperature and CO_2 in healthy, unstressed plants, exist within the plant kingdom. On an area basis, values of A cover a wide range, from less than 2 up to 70 µmol CO_2 m^{-2} s^{-1} (Larcher, 1995), and may even achieve values as high as 80 µmol CO_2 m^{-2} s^{-1}, as in *Amaranthus retroflexus* (Pearcy and Ehleringer, 1984). However, it is often difficult to make meaningful comparisons of photosynthetic rates as determined by different investigators because of variations in measurement techniques and methods of expressing photosynthetic rates, in addition to preconditioning effects of environment on leaf anatomy (Kozlowski and Pallardy, 1997).

Comparative studies of C_3 and C_4 plants have generally shown that the latter, in their native habitats, exhibit higher photosynthetic rates. Such a behaviour is largely a result of a suite of biochemical, physiological and morphological components collectively functioning to concentrate CO_2 in vascular bundle sheath cells (Pearcy and Ehleringer, 1984). On the other hand, the majority of C_3 plants, particularly woody species, display low photosynthetic performances (Körner, 1995; Larcher, 1995). However, some agricultural C_3 crop plants may achieve photosynthetic rates near or similar to those of C_4 species, possibly due to

successful breeding (Larcher, 1995). On biochemical grounds, the causes of the specific differences in A lie in the capacity of ribulose-1,5-bisphosphate (RuBP) carboxylase to consume RuBP, the capacity of the thylakoid and Calvin cycle reactions to regenerate RuBP, and the capacity of starch and sucrose synthesis to regenerate inorganic phosphate from phosphorylated photosynthetic intermediates. Each of these processes represents major points of direct interaction with the environment beyond the photosynthetic apparatus (Sage and Reid, 1994).

Some investigations have been conducted in order to characterise the photosynthetic performance of a given species or a community. In several cases a high correlation between leaf nitrogen concentration and A of different species has been found (Field and Mooney, 1986; Chazdon and Field, 1987; Evans, 1989; Reich and Walters, 1994; Woodward and Smith, 1995). Other studies have shown a high correlation between leaf conductance and A within diverse vegetation types distributed world-wide (Körner *et al.*, 1979; Körner, 1995). Comparatively with A, to our knowledge less is known about the characterisation of potential photosynthetic rates (A_{pot}), which herein represent the rate of net photosynthesis as measured at optimal temperature under saturating PPF and CO_2. Previous results obtained in our laboratory with some tropical species revealed very similar values of A_{pot} among species, despite large differences in A among them. It remains to be

ascertained, therefore, whether A_{pot} shows a conservative pattern among plants of different photosynthetic performances. In this preliminary work, A and A_{pot} were measured in 14 C_3 and C_4 tropical crop species, including herbaceous and woody plants which differ widely in growth habit, leaf anatomy and photosynthetic capacity. For comparison, a C_4 dicot, *Amaranthus* sp., a weed plant commonly occurring in disturbed habitats and agricultural fields, was also investigated.

MATERIAL AND METHODS

Plant material and growth conditions

Photosynthetic measurements were conducted on ten C_3 species, including one monocot, rice (*Oryza sativa* L.), four herbaceous dicots, common bean (*Phaseolus vulgaris* L.), soybean (*Glycine max* [L.] Merr.), sunflower (*Helianthus annuus* L.) and cotton (*Gossypium hirsutum* L.), one shrub, cassava (*Manihot esculenta* Crantz), and four tree dicot plants, cacao (*Theobroma cacao* L.), coffee *(Coffea arabica* L.), rubber (*Hevea brasiliensis* [H.B.K.] Muell-Arg.) and eucalyptus (*Eucalyptus urophylla* Blake × *E. grandis* Hill ex Maiden). Five C_4 species were also used, including one dicot, pigweed (*Amaranthus* sp.), and four monocots, panic grass (*Panicum maximum* Jacq.), millet (*Pennisetum purpureum* Schumach), maize (*Zea mays* L.) and sugarcane (*Saccharum officinarum* L.). Eucalyptus, cassava and sugarcane were grown from stem cuttings, and the remaining species were raised from seeds.

The experiment was carried out in Viçosa (20^o45'S, 650 m a.s.l.), Brazil, in a greenhouse at ambient CO_2 without temperature control. At 13h00, air temperature inside the greenhouse was up to 7 ^{o}C higher than outside air. Incoming PPF was transmitted by 60%, as determined in mid-summer. Plants were grown in 6-L plastic pots containing a 3:1 (v:v) mixture of soil and manure. In order to get uniform plants, the seedlings were thinned after germination. Plants were watered daily and flushed once a week with 400 mL of full strength Hoagland solution (Hoagland and Arnon, 1950). At the time of measurements, the herbaceous plants, employed prior to flowering, were four to six weeks old, and the young tree species were eight to 13 months old. Cassava was approximately two months old. All measurements were made in late spring or in summer on a youngest, completely expanded mature leaf or leaflet.

Leaf gas exchange parameters

The stomatal conductance to water vapour (g_s) and A were measured on attached leaves at ambient CO_2 partial pressure (about 36 Pa) using a portable, open-system infrared gas analyser (LCA-4, Analytical Development Co., Hoddesdon, UK). Artificial PPF was supplied by a portable light unit (PLU2-002) containing a dichroic 12 V, 20 W lamp, an air extractor fan and an infrared heat absorbing filter. For C_3 species, PPF for saturating photosynthesis was determined from response curves of A to PPF obtained in triplicates for each species; such a saturating PPF varied from 650-750 μmol m^{-2} s^{-1} as in cacao and coffee, respectively, to 1700 μmol m^{-2} s^{-1} as in sunflower. For C_4 species, photosynthesis was not fully saturated by employing the maximum attainable PPF of almost 2000 μmol m^{-2} s^{-1}. After fitting the leaf tissue in the Parckinson leaf chamber (PLC4), rates for gas exchange were typically settled within 2-3 min, nearly paralleling stabilisation for internal CO_2 values. Gas flow through the leaf chamber was 255 ± 2 μmol s^{-1}. During the measurements (08h30-09h30), the air relative humidity and leaf temperature ranged from 74 to 83%, and 24 to 29°C, respectively.

Potential photosynthetic rates (A_{pot}) were measured by oxygen evolution on the same leaves used for A measurements, and determined under saturating CO_2 partial pressure (approximately 5 kPa supplied by 0.2 mL of 1 kmol m^{-3} $KHCO_3$), using a gas-phase oxygen electrode (LD-2 Leaf Chamber,

Hansatech, Norfolk, UK). PPF was provided by a 200 W halogen-tungsten bulb mounted in a light source (LS2, Hansatech), which gave little less than 3000 μmol m^{-2} s^{-1}. Saturating PPF at the leaf disk surface (1500-2600 μmol m^{-2} s^{-1}) was adjusted by using neutral density filters. Maximum values of A_{pot} were measured at 35 ^{o}C following response curves of A_{pot} to temperature obtained in triplicates for all species. Photosynthetic rates were also measured at saturating light and CO_2, but at the same average leaf temperature at which A was measured (A_{max}). When possible, A_{max} and A_{pot} were determined in 10 cm^2 leaf discs; in other cases leaf slices were used, and their total area for photosynthetic rate calculations was measured using an area meter (Area Measurement System, Delta-T Devices, Cambridge, UK). Leaf pieces were then dried to constant mass at 70 ^{o}C in order to determine their specific leaf area (SLA). This parameter was used to express photosynthetic rates per unit mass.

Statistical analysis

Statistical significance among means obtained from 12 replicates was determined using an ANOVA analysis with a Newman-Keuls' post-test to examine if significant ($P < 0.05$) differences occurred between individual means. In some cases, non-orthogonal contrasts were used in order to confront the overall means from certain groups of plants (*e.g.*, woody species against the remaining ones) using a Scheffé's test.

RESULTS AND DISCUSSION

As Table 1 shows, A per unit area varied widely among the species investigated, from 5.0 up to 26.3 μmol CO_2 m^{-2} s^{-1}. As expected, C_4 plants exhibited the greatest values of A, although sunflower had values similar to plants of the C_4 group, likely as a result of its high g_s (Table 1) and high amounts of Rubisco (Larcher, 1995). Tree species showed the lowest A; in eucalyptus, however, A laid in the range of herbaceous C_3 plants, probably as a consequence of its unusually large g_s (Table 1). Differences in A, particularly

amongst the C_3 plants, might be to some extent attributed to differences in g_s. Nonetheless, values of A, particularly for C_4 species, were in general lower than those reported elsewhere (*e.g.*, Gifford, 1974; Ziska and Bunce, 1997). This might in part be a consequence of relatively high temperatures inside the greenhouse.

When rates of photosynthesis were measured at saturating CO_2 (A_{max}), a different pattern emerged (Table 1). In general, the differences in A_{max} amongst species were quite narrow, and hence variations in A_{max}/A ratio were due chiefly to changes in A. In C_4 plants that ratio ranged from 1.05 to 1.12, indicating that photosynthesis is almost saturated at ambient CO_2. In C_3 species A_{max}/A ratio laid between 1.31 and 5.40 (Table 1). In other words, the rates of photosynthesis under saturating CO_2 could be up to 440% above those found at current atmospheric CO_2 partial pressure, as was the case of rubber seedlings. Because A_{max} was determined under saturating CO_2, minimal or no limitation to CO_2 diffusion from the outside atmosphere to the carboxylation sites in the chloroplasts and the inhibition of photorespiration are to be expected. These facts undoubtedly contributed to the similarity of values of A_{max} observed among the species investigated.

It should be stressed that slight differences in leaf temperature between measurements of A and A_{max} occurred and therefore the values of these parameters among the species examined might not be rigorously comparable. Regardless of the wide variations in A, A_{pot} (measured at 35 ^{o}C) per unit area was very similar for all species except for cacao, in which it was significantly lowered (42%; $P < 0.0001$) than the overall mean A_{pot} (35 ± 2.4 μmol O_2 m^{-2} s^{-1}) of the remaining 14 species (Table 1). The results obtained with cacao should, however, be interpreted cautiously because, as opposed to the other species, cacao seedlings display several shade adaptation attributes. For example, although being cultivated under the same light regime, cacao leaves showed a significant ($P < 0.0001$) doubling in SLA in comparison with the mean SLA from the other three tree species (Table 2). Thus, it is,

TABLE 1 - Stomatal conductance to water vapour (g_s), actual photosynthetic rate determined under non-limiting light at ambient temperature and CO_2 (A), photosynthetic rate measured under saturating light and CO_2 at the same average leaf temperature at which A was measured (A_{max}), and potential photosynthetic rate gauged at optimal temperature under saturating light and CO_2 (A_{pot}) of 15 tropical crop species. Photosynthetic parameters are means of 12 replicates expressed on an area basis. Values followed by the same letter in the column do not differ statistically by the Newman-Keuls' test ($P > 0.05$).

Species	g_s mmol m^{-2} s^{-1}	A μmol m^{-2} s^{-1}	A_{max} μmol m^{-2} s^{-1}	A_{max}/A	A_{pot} μmol m^{-2} s^{-1}
Maize	140 gh	23.4 a	26.0 ab	1.11	34.7 a
Panic grass	141 gh	22.3 a	23.5 ab	1.05	33.0 a
Millet	210 def	25.0 a	27.3 ab	1.09	33.4 a
Sugarcane	164 fg	24.0 a	25.2 ab	1.05	33.9 a
Pigweed	209 def	26.3 a	29.4 ab	1.12	35.0 a
Sunflower	585 a	24.6 a	32.2 a	1.31	38.7 a
Soybean	272 cde	18.3 bc	25.0 ab	1.37	34.0 a
Common bean	203 ef	16.3 cd	31.9 a	1.96	37.5 a
Rice	374 b	10.3 ef	25.7 ab	2.50	31.1 a
Cotton	230 def	18.2 c	31.8 a	1.75	39.3 a
Cassava	198 fg	13.7 de	23.1 bc	1.69	35.7 a
Eucalyptus	320 bcd	14.4 cd	26.1 ab	1.81	33.4 a
Coffee	88 hi	5.9 g	23.8 ab	4.03	33.1 a
Rubber tree	67 i	5.0 g	27.0 ab	5.40	37.3 a
Cacao	120 hi	6.9 fg	14.7 c	2.13	20.4 b

TABLE 2 - Specific leaf area (SLA) of 15 tropical species. Values are means of 12 replicates. Means followed by the same letter in the columns do not differ statistically by the Newman-Keuls' test ($P > 0.05$).

Species	SLA $m^2 kg^{-1}$	Species	SLA $m^2 kg^{-1}$
Maize	26.0 a	Rice	25.2 a
Panic grass	20.7 b	Cotton	16.7 cd
Millet	20.3 b	Cassava	20.7 b
Sugarcane	19.4 bc	Eucalyptus	13.0 2e
Pigweed	21.4 b	Coffee	14.6 de
Sunflower	25.0 a	Rubber tree	11.6 e
Soybean	19.5 bc	Cacao	25.2 a
Common bean	19.0 bc		

possible that the differential behaviour of A_{pot} in cacao might be a consequence of its native origin and domestication as understory, shade trees which commonly exhibit low light-saturated photosynthetic rates as a result of low concentration of photosynthetic enzymes and electron transport carriers per unit area (Chazdon *et al.*, 1996). Coffee, on the other hand, in spite of its being originated in natural shady habitats, has a high photosynthetic plasticity, being successfully cultivated at full sun, as in Brazil. With the exception of A_{pot} for cacao plants, the present results suggest that the photosynthetic potential of individual leaves on an area basis might be a conservative attribute amongst the tropical species here investigated. This pattern should not be attributed to inhibitory effects of high CO_2 on respiration (Saralabai *et al.*, 1997), or to respiration per se, as no consistent difference in respiratory rates under either normal or high CO_2 was found amongst the species studied (not shown). Although the results obtained here refer to only one

developmental stage under one set of growth conditions, in a side experiment the overall rate of A_{pot} per unit area of field-grown panic grass, millet, sugarcane, pigweed, cassava, coffee and rubber tree was 34.8 ± 3.9 µmol O_2 m^2 s^{-1}, within the same range of values of the present study. A similar rate with hydroponically-cultured common bean at pod formation stage was also found (Lima *et al.*, 2000), supporting the suggestion of a conservative behaviour of A_{pot}.

The most satisfactory basis for expressing photosynthetic rates apparently is leaf area (Kramer and Kozlowski, 1979). However, area-based photosynthesis may be misleading because thick leaves may have more chloroplasts per unit surface than thin leaves; therefore a high rate of CO_2 uptake per unit area would be expected, regardless of what would cause the difference in thickness (Kramer and Kozlowski, 1979; Brown, 1994). In fact, mass-based photosynthesis and SLA are usually negatively related to each other (Reich *et al.*, 1991; Prado and Moraes, 1997). Hence, the variations in *A* per unit area in the present work, in addition to those attributable to g_s, could have arisen in part from differences in SLA (Table 2). Nonetheless, *A* per unit area and SLA showed a trend to change in the same direction, although the correlation between these parameters was not significant ($P > 0.05$). By expressing *A* per unit mass (Table 3), the differences in photosynthetic rates among species were markedly larger than those of *A* per unit area. On the other hand, the variations of A_{pot} per unit mass were not so large, with a little more than a doubling between the lowest and the highest value of A_{pot} obtained with rubber tree and sunflower, respectively (Table 3). Again, this fact also lends support to the hypothesis that A_{pot}, whether considered on either an area or a mass basis, is a conservative attribute in the species investigated.

By contrasting the tree species with the remaining ones, mass-based A_{pot} was significantly ($P < 0.001$) lower in the tree species, these producing an overall A_{pot} of 28.0 ± 2.2 µmol O_2 g^{-1} min^{-1} against 44.6 ± 5.8 µmol O_2 g^{-1} min^{-1} for the other species. This difference was markedly

associated with the low SLA in tree species (except cacao). It should be emphasised, however, that low SLA, particularly in woody plants, could result

TABLE 3 - Actual photosynthetic rate determined under non-limiting light at ambient temperature and CO_2 (*A*), and potential photosynthetic rate measured at optimal temperature under saturating light and CO_2 (*A*$_{pot}$) of 15 tropical crop species. Photosynthetic rates are means of 12 replicates expressed on a dry mass basis. Values followed by the same letter in the column do not differ statistically by the Newman-Keuls' test (*P* > 0.05).

Species	*A*, μmol g^{-1}min^{-1}	*A*$_{pot}$, μmol g^{-1}min^{-1}
Maize	34.3 ab	53.8 ab
Panic grass	27.6 d	41.5 cd
Millet	30.3 bcd	40.6 cdef
Sugarcane	29.1 cd	39.5 cdef
Pigweed	33.5 abc	45.0 bc
Sunflower	37.3 a	56.5 a
Soybean	21.9 e	40.0 cdef
Common bean	19.0 ef	42.8 cdef
Rice	15.9 f	47.2 abc
Cotton	18.2 f	39.5 cdef
Cassava	17.0 f	44.4 bc
Eucalyptus	11.1 g	26.4 g
Coffee	5.2 h	29.3 efg
Rubber tree	3.5 h	26.0 g
Cacao	10.4g	30.4 defg

from an increased investment in non-photosynthetic tissues throughout their long leaf life-spans (Bongers and Popma, 1990; Reich and Walters, 1994).

In addition, lower SLA and longer leaf life-span have been also associated with (1) potentially different infra-leaf allocation of nitrogen; (2) greater within-leaf shading; and (3) potential diffusion limitations to net carbon uptake (Poorter and Evans, 1998; Reich *et al.*, 1998). These leaf traits might also explain in part why *A* per unit area varied about 5-fold in contrast to a 10-fold variation in *A* per unit mass among the species studied. Therefore, this might be an important point for explaining the relatively lower *A*$_{pot}$ as expressed on a mass basis of tree species.

In conclusion, the results suggest that regardless of the basis used for expressing *A*$_{pot}$, the instantaneous potential photosynthetic rates for carbon fixation were similar among a variety of C_3 and C_4 tropical crop species studied here. Of course, the similarity in *A*$_{pot}$ values within these species was accounted for only by pre-existing components of the photosynthetic apparatus, as other attributes, such as enzyme amounts, would hardly have changed after short-term exposure (5-10 min) of leaves to saturating CO_2. In any case, the similar values of *A*$_{pot}$ might have resulted from a conservative potential to fix CO_2. Hence, the large differences in *A* observed here should be attributed to differential limitations to the overall photosynthetic process, and not to the photosynthetic capacity *per se*.

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