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Oxygen Stimulation of Apparent Photosynthesis in *Flaveria linearis*[1]

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ABSTRACT

A plant was found in the C_3-C_4 intermediate species, *Flaveria linearis*, in which apparent photosynthesis is stimulated by atmospheric O_2 concentrations. A survey of 44 selfed progeny of the plant showed that the O_2 stimulation of apparent photosynthesis was passed on to the progeny. When leaves equilibrated at 210 milliliters per liter O_2 were transferred to 20 milliliters per liter O_2 apparent photosynthesis was initially stimulated, but gradually declined so that at 30 to 40 minutes the rate was only about 80 to 85% of that at 210 milliliters per liter O_2. Switching from 20 to 210 milliliters per liter caused the opposite transition in apparent photosynthesis. All other plants of *F. linearis* reached steady rates within 5 minutes after switching O_2 that were 20 to 24% lower in 210 than in 20 milliliters per liter O_2. At low intercellular CO_2 concentrations and low irradiances, O_2 inhibition of apparent photosynthesis of the aberrant plant was similar to that in normal plants, but at an irradiance of 2 millimoles quanta per square meter per second and near 300 microliters per liter CO_2 apparent photosynthesis was consistently higher at 210 than at 20 milliliters per liter O_2. In morphology and leaf anatomy, the aberrant plant is like the normal plants in *F. linearis*. The stimulation of apparent photosynthesis at air levels of O_2 in the aberrant plant is similar to other literature reports on observations with C_3 plants at high CO_2 concentrations, high irradiance and/or low temperatures, and may be related to limitation of photosynthesis by triose phosphate utilization.

Inhibition of AP[2] by O_2 is a well documented phenomenon in C_3 plants and results from competition between O_2 and CO_2 for RuBP during CO_2 assimilation plus the oxidation of glycolate to yield CO_2 in the photorespiratory cycle (6). The extent of inhibition of AP by atmospheric O_2 concentration is about 30% in C_3 species when tested near atmospheric levels of CO_2 (2). Some species classified as C_3-C_4 intermediates are less sensitive, their AP being inhibited by about 20% at atmospheric levels of O_2 (3, 11, 14). *Flaveria linearis* is one of the C_3-C_4 species found to have lower O_2 inhibition than C_3 species (14).

Because CO_2 and O_2 compete for reaction with RuBP, AP of leaves of C_3 species are generally O_2-insensitive at high CO_2 concentrations (1, 5, 18), but in some cases AP has been slightly higher at 210 ml L^{-1} than at lower O_2 levels (5, 8, 12, 15, 18, 20, 21). It has been suggested that O_2 is required to sustain a high rate of photophosphorylation to support AP at high CO_2 concentrations (5). Sharkey (17, 18) recently postulated that O_2-insensitivity of AP may result from AP being limited by TPU. If AP at 210 ml L^{-1} O_2 is limited by utilization of triose phosphates rather than by substrate levels (RuBP or CO_2) then it is predicted that reducing O_2 around the leaf would not increase AP. According to Sharkey (17, 18), shortage of Pi may be involved in the limitation because of accumulation of phosphate in carbon cycle intermediates. It has been observed that when Pi is sequestered by infiltrating mannose into spinach leaf discs O_2 sensitivity of AP is lost (10). The shortage of Pi may be exacerbated by low O_2 since under conditions of O_2-insensitivity of AP, lowering O_2 concentration has been found to raise the levels of RuBP and 3-P-glyceraldehyde (TD Sharkey, personal communication). Therefore, under conditions of TPU limitation, O_2 may have no effect or may actually stimulate AP because less Pi is tied up in phosphorylated intermediates and phosphoglycolate produced by reaction of O_2 and RuBP is also a source of Pi.

O_2-insensitivity or stimulation of AP has been observed only at low temperatures (8, 12), at CO_2 levels above atmospheric (12, 17, 18, 20, 21), or at concentrations near atmospheric in plants under stress (18). In this paper we report the O_2 response of AP in a plant of the species, *F. linearis*, in which AP is stimulated by 210 ml L^{-1} O_2 at atmospheric CO_2 concentrations, and under nonstress growth conditions.

MATERIALS AND METHODS

Plant Material. Seeds of *Flaveria linearis* were kindly supplied by Dr. M. S. B. Ku, Washington State University. When several plants grown from these seed were tested for O_2 inhibition of AP at 320 μl L^{-1} CO_2 all exhibited about 20% inhibition by 210 ml L^{-1} O_2 compared to 20 ml L^{-1}, except one plant designated 84-9, in which AP was either O_2-insensitive or was lower at 20 ml L^{-1} than 210 ml L^{-1} O_2. This plant was propagated vegetatively and grown in 3-L pots filled with a 1:1:1 (by volume) mixture of peat:soil:Perlite. Other plants from the same seed lot were handled in the same way. In addition, for some experiments plants of the C_4 species *Flaveria trinervia* (14) and the C_3 species *Panicum boliviense* (4) were grown under the same conditions for comparison to *F. linearis*. Plants were grown in a greenhouse in which temperatures ranged from a maximum of 30 to 35°C during the d to a minimum of about 25°C at night. They were grown during summer when maximum irradiance at midd was 1.5 to 2.2 mmol quanta m^{-2} s^{-1} PAR. Plants were fertilized twice weekly with full strength Hoagland solution.

Gas Exchange Measurements. Measurements of AP and transpiration were made in acrylic plastic chambers 13 cm long, 7 cm wide, and 7.5 cm deep. The chambers had a removable top which was held in place by bolts and wing nuts. Soft closed-cell plastic gaskets provided an effective seal when leaves were enclosed. The chamber was separated into two compartments by

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[2] Abbreviations: AP, apparent photosynthesis; RuBP, ribulose bisphosphate; TPU, triose phosphate utilization; c_i, intercellular CO_2 concentration.

an acrylic plastic partition which had a 2.5 cm diameter hole in each end. The upper compartment was 1 cm deep and the lower was 6.2 cm deep. A fan and a cooling coil was installed in the bottom compartment, and air was circulated over the coil, through the hole in the opposite end of the partition, and past the leaf enclosed in the upper compartment. Water was circulated through the cooling coil from a temperature controlled bath. A fine wire thermocouple was pressed against the lower side of the enclosed leaf. Four similar chambers were arranged in a circle under a 1500 W multivapor lamp and a switching system was used to sequentially monitor chambers for exhaust gas and temperature for 5 min periods. Thus, four leaves could be measured in one experiment.

Prepared gas mixtures were humidified to a dewpoint of 11 to 13°C (constant to within 0.3°C for a given experiment) by passing first through a flask containing water and then through a water cooled condenser. Transpiration raised the dewpoint in the chamber to 17 to 24°C. Water vapor and CO_2 differentials in intake and exhaust gas were measured with a dewpoint hygrometer and an IR gas analyzer, respectively. Water vapor and CO_2 exchange were calculated from flow rates and concentration differentials in intake and exhaust air. Leaf temperature was maintained at 30°C and incident PAR was 2 mmol quanta m^{-2} s^{-1}, except in the experiment involving light response. All AP measurements were made on the youngest fully expanded leaf on vegetative shoots.

Variation in O_2 Sensitivity of AP within the Genotype. *F. linearis* 84-9 was self-pollinated by dusting the inflorescence with pollen collected from several 84-9 plants, using a small, soft bristle brush. Seeds produced were germinated and plants were cultured as in the previous section, except the pots were smaller (1L). Forty-four plants were tested for O_2 inhibition of AP when they had grown to a height of 10 to 20 cm.

Testing was done by measuring AP at 20 and 210 ml L^{-1} O_2. Measurements were made at CO_2 concentrations and dewpoints in the leaf chamber which ranged from 295 to 315 μl L^{-1} and 17 to 21°C, respectively. For a given leaf, CO_2 concentrations in the chamber never differed more than 10 μl L^{-1} for comparison of AP at 20 and 210 ml L^{-1} O_2 and the differences were usually less than 5 μl L^{-1}. Leaf area in the chamber ranged from 2.5 to 5.0 cm^{-2}. The measurements of AP were repeated on three separate leaves of each plant.

Time Course of AP after Changes in O_2 Concentration. Compressed gas cylinders were prepared with mixtures containing 335 μl L^{-1} CO_2, and 20 or 210 ml L^{-1} O_2, with the balance N_2. One of the chambers described under the gas exchange measurement section was used, and AP was monitored continuously. The leaf chamber was flushed at a rate of 0.4 L min^{-1} with 20 or 210 ml L^{-1} O_2 until steady state AP was attained. The gas stream was then quickly changed with a switching valve to the other O_2 concentration and AP was followed for 25 min in the first set of measurements and 40 min in others with a constant flow rate. Responses of a plant produced from seed of 84-9 (designated 84-9s), and one from rooted cuttings of *F. linearis* (84-5) were compared. Measurements were made on three leaves of each plant after switching from 20 to 210 ml L^{-1} and three leaves of 84-9s and two of 84-5 after switching from 210 to 20 ml L^{-1} O_2. Rates of AP were calculated at 5 min intervals after switching O_2 concentrations. The chamber was fully flushed at 2 to 3 min after switching.

Light Response of AP. Measurements of AP were made at irradiances of 0.2, 0.45, 0.8, and 2.0 mmol quanta m^{-2} s^{-1}. Irradiance was varied by placing plastic shade screens over the leaf chamber. At each irradiance AP was measured at 20 and 210 ml L^{-1} O_2, on three leaves of *F. linearis* (84-5) and three leaves each of two plants grown from seed of 84-9 (84-9s). Concentrations of CO_2 in the leaf chamber were maintained in the range of 310 to 340 μl L^{-1} (the higher concentrations at the lowest irradiance) and dewpoint was kept in the range of 17 to 22°C. For two leaves of each plant the irradiance was changed stepwise from highest to lowest and in the third from lowest to highest. The sequence did not appear to influence the response.

Response of AP to CO_2 Concentrations. The response of AP to CO_2 concentration was determined by measurements at 20 ml L^{-1} O_2 and CO_2 concentrations entering the leaf chamber of 83, 125, 207, 335, and 500 μl L^{-1}. Measurements at 210 ml L^{-1} O_2 were made with gases containing 83, 113, 210, 328, and 487 μl L^{-1} CO_2. Concentrations of CO_2 leaving the chamber were assumed to represent that surrounding the leaf, since the air was well stirred in the chamber; c_i was calculated from leaf conductance derived from transpiration. Dewpoints in the leaf chamber ranged from 17 to 22°C during the experiment, and for a given leaf the variation was 2°C or less.

Response of AP to CO_2 was determined for *F. linearis* (plants 84-9, 84-5, 84-7, and 84-8), *F. trinervia* (C_4), and the C_3 species *Panicum laxum* (4). Response curves were established for three separate leaves of each plant, except *F. linearis* 84-9, for which five leaves were measured. Since the response was similar for *F. linearis* 84-5, 84-7, and 84-8 the data for these were averaged.

RESULTS

The influence of 210 ml L^{-1} O_2 on AP in progeny of *Flaveria linearis* 84-9 ranged from 12.7% inhibition to 27.3% stimulation (data not shown). Of the 44 plants tested, however, only three had O_2 inhibition of AP, with values of 3.7, 5.8, and 12.7%. Response of steady state AP to O_2 for none of the plants approached the 20 to 24% O_2 inhibition in other *F. linearis* plants (Fig. 1). There was a range of AP at 210 ml L^{-1} O_2 from 13.4 to 27.4 mmol CO_2 m^{-2} s^{-1}, but AP rate was not related to O_2 response.

The stimulation of AP by O_2 in plant 84-9s was not immediate upon switching from 20 to 210 ml L^{-1} or vice versa. There was an initial (5 min after switching) inhibition of AP in two or three leaves upon changing from 20 to 210 ml L^{-1} O_2 and AP was initially stimulated upon changing from 210 to 20 ml L^{-1} O_2 (Fig. 1). Inhibition of AP by 210 ml L^{-1} O_2 and stimulation by 20 ml L^{-1} disappeared with time after switching, rapidly for about 20 min and more slowly for an additional 20 min. After 40 min, stimulation of AP by 210 ml L^{-1} O_2 was 20 to 25%. In contrast to plant 84-9s, AP of *F. linearis* 84-5 was inhibited 20 to 24% by 210 ml L^{-1} O_2 and stimulated 27 to 30% by low O_2 and the O_2 effect was constant from 5 to 40 min after changing

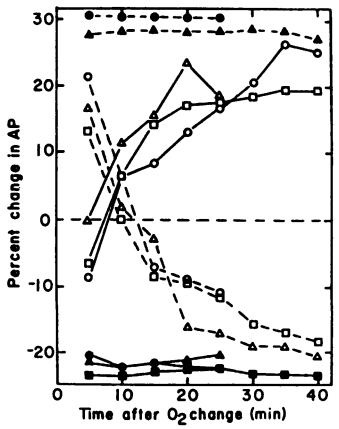

FIG. 1. Percent change in AP at various times after switching from 210 to 20 ml L^{-1} O_2 (– – –) and from 20 to 210 ml L^{-1} O_2 (——) for *F. linearis* 84-5 (●, ■, ▲) and selfed progeny of 84-9 (○, □, △). Measurements were made at 2.0 mmol quanta m^{-2} s^{-1}, 30°C and 335 μl L^{-1} CO_2. Different symbols represent separate leaves.

O_2 concentrations. This degree of O_2 inhibition at atmospheric CO_2 levels is consistent with other data for C_3-C_4 species (4, 11).

The stimulation of AP by O_2 occurred only at high irradiances. At the lowest irradiance AP of all three *F. linearis* plants was inhibited about 30%, a value typical of C_3 species (Fig. 2A). Upon raising the irradiance to 2 mmol quanta m^{-2} s^{-1}, AP was inhibited 19.5% by O_2 in plant 84-5, whereas, AP of the two 84-9s plants was stimulated by 20 to 25%. The influence of O_2 on AP in the 84-9s plants changed steadily with increasing irradiance, whereas in 84-5 inhibition of AP remained nearly constant at 30% until irradiance was raised above 0.8 mmol quanta m^{-2} s^{-1}.

In contrast to most C_3 species and to plant 84-5 in Figure 2, AP in the 84-9s plants was saturated at lower irradiances with 20 than with 210 ml L^{-1} O_2 (Fig. 2B). Because of this, AP became higher at 210 than 20 ml L^{-1} O_2 at about 1.1 mmol quanta m^{-2} s^{-1} in one 84-9s plant and about 0.65 mmol quanta m^{-2} s^{-1} in the other. Stimulation of AP by O_2 occurred at a lower irradiance in the plant that had the lower maximum AP rate.

The response of AP to CO_2 was similar in 84-9 and other *F. linearis* plants at low c_i, but at c_i above 100 μl L^{-1} the divergence is remarkable (Fig. 3). Whereas for normal *F. linearis* plants AP was a linear function of c_i up to about 200 μl L^{-1} and with some curvature to about 325 μl L^{-1}, AP at 210 ml L^{-1} O_2 in 84-9 was CO_2 saturated at about 225 μl L^{-1}. At 20 ml L^{-1} O_2 there was a sharp break in the response of AP at a c_i of 100 μl L^{-1} and a decrease in AP with further increases in c_i. The maximum AP at 20 ml L^{-1} O_2 was only about 50% as high for plant 84-9 as for the other *F. linearis* plants. Data (not shown) for *F. trinervia* (C_4) and *P. laxum* (C_3) were similar to that previously published for C_4 and C_3 species (2). The C_4 species showed no O_2 sensitivity at any CO_2 concentration and AP saturated at about 100 μl L^{-1} c_i. In *P. laxum* AP was inhibited about 35% by 210 ml L^{-1} O_2 at a c_i, (200 μl L^{-1}) in approximate equilibrium with atmospheric CO_2.

DISCUSSION

The plant *Flaveria linearis* 84-9 has an O_2 sensitivity of AP different from other plants in the species and also unique among

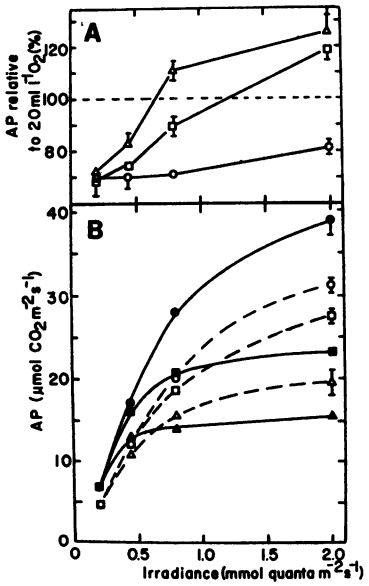

FIG. 2. Response of AP in *F. linearis* to irradiance at 210 (- - -) and 20 ml L^{-1} O_2 (——) (B), and the change in AP at 210 ml L^{-1} O_2 relative to that at 20 ml L^{-1} O_2 as a function of irradiance (A). *F. linearis* 84-5 is represented by (○, ●), and two selfed progeny of *F. linearis* 84-9 are represented by (△, ▲, □, ■). Vertical bars are ±1 SD. AP was measured at 30°C and 310 to 340 μl L^{-1} CO_2.

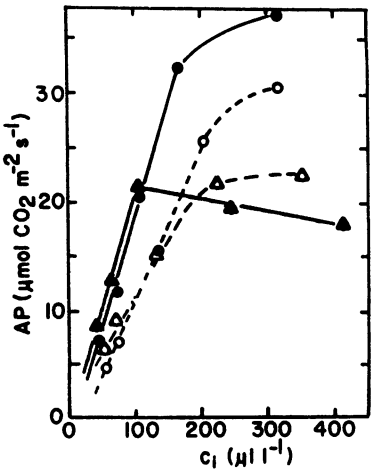

FIG. 3. Response of AP in *F. linearis* to c_i at 20 (——) and 210 ml L^{-1} O_2 (- - -). (○, ●), average AP for three leaves each of plants 84-5, 84-7 and 84-8. (△, ▲), averages of measurements of five leaves of 84-9. Measurements made at 30°C and 2 mmol quanta m^{-2} s^{-1}.

plants reported in the literature. This unique response is most clearly demonstrated as a stimulation of AP by O_2 at atmospheric levels of CO_2, high irradiance, and near optimum temperature. This is in contrast to all other species reported, which under these conditions show either O_2 inhibition of AP as in C_3 and C_3-C_4 species or a lack of O_2 sensitivity characteristic of C_4 species, CAM species during nocturnal CO_2 assimilation, and some algae (2, 4, 6, 11, 12).

In characteristics other than CO_2 exchange plant 84-9 appears similar to other *F. linearis* plants with which we have compared it. Floral and foliar characteristics are identical to those of other plants from the same seed source. Leaf anatomy and CO_2 compensation concentrations are not distinguishable from other *F. linearis* plants (data not shown).

Plant 84-9 is easily distinguishable in the magnitude of AP and especially its response to CO_2, irradiance, and O_2. In the test of 84-9 progeny the average AP at 210 ml L^{-1} O_2 was 21.6 ± 2.3 μmol CO_2 m^{-2} s^{-1} which along with data in Figures 2B and 3 indicate that this plant had about 70 to 80% of the AP of other *F. linearis* plants. In plant 84-9, AP was saturated at lower c_i and irradiance than other *F. linearis* plants. The lower AP and lower CO_2 and irradiance levels required for saturation, along with O_2 stimulation of AP, may indicate TPU limitation of AP suggested by Sharkey (17, 18).

A stimulation of AP by O_2 has been reported in some C_3 species under conditions of high CO_2, high irradiance, and/or low temperature (5, 8, 12, 14, 15, 17, 18). However, no reports of O_2 stimulation of AP have been made for temperatures as high as 30°C with c_i as low as 200 μl L^{-1}. In addition, inhibition of AP by exposure to low O_2 has in several cases been transitory, with recovery requiring only a few minutes (5, 15, 20). Response of AP of 84-9 to CO_2 and O_2 concentrations most closely resembles the results of Cornic and Louason (8) for measurements conducted with C_3 species at 5°C. They observed stimulation of AP by 210 ml L^{-1} O_2 at CO_2 concentrations of 200 to 400 μl L^{-1} or higher. In most other reports, much higher CO_2 concentrations were required (5, 15, 18, 21). Some of the variation in conditions required for O_2 stimulation of AP is undoubtedly due to the way plants were grown and experimental protocol. The stimulation in 84-9, however, is not due to growth or experimental conditions, since other plants under the same conditions did not show O_2 insensitivity or stimulation of AP.

Sharkey (17, 18) proposed that in addition to the limitation of AP by RuBP carboxylase activity and RuBP regeneration, AP could also be limited by TPU. This limitation was postulated to

occur when the capacity of a leaf to convert triose phosphates to starch or sucrose is reached. Under this limitation Pi would be accumulated in carbon cycle intermediates and Pi in the chloroplast would drop below the level required for photophosphorylation. Limitation by TPU is most likely to occur at high irradiance and CO_2 concentrations when synthesis of triose phosphates is high or under stress conditions when utilization of photosynthetic products is low. Under these conditions, reducing O_2 concentration would not stimulate AP because the rate is limited by utilization of photosynthetic products rather than by substrate levels or activation of RuBP carboxylase.

As shown by Sharkey (18) for plants with O_2-insensitivity, photorespiration was probably occurring in plant 84-9 under conditions of O_2 stimulation of AP. This is indicated by the initial inhibition of AP when leaves equilibrated at 20 ml L^{-1} O_2 were switched to 210 ml L^{-1} O_2. Switching from 210 to 20 ml L^{-1} O_2 also caused an initial stimulation of AP. In fact, the rate of change in AP from 5 to 10 min after switching O_2 levels (Fig. 1) indicates that the initial effect of switching may have been similar to that in the other *F. linearis* plants. So RuBP oxygenation rates in plant 84-9 may be similar to those in other *F. linearis* at high as well as low CO_2 concentrations.

Higher photophosphorylation and consequently greater RuBP synthesis has been suggested as the cause of higher AP when O_2 is increased (5, 15). Since O_2 stimulation in plant 84-9 occurs at CO_2 levels where RuBP limitation is most likely, this suggestion implies that AP would be increased at 210 ml L^{-1} O_2 due to increased RuBP pool size. However, evidence that RuBP levels in leaves are higher at 210 than 20 ml L^{-1} O_2 is not available and most published data show the opposite. In spinach protoplasts (7) and soybean and bean leaves (1, 9) RuBP levels decreased as O_2 was increased. In wheat leaves O_2 had little effect on RuBP concentration at 350 and 1400 μl L^{-1} CO_2, but at 100 μl L^{-1} CO_2 RuBP was decreased in 210 compared to 1 ml L^{-1} O_2 (16). Thus, it appears that RuBP levels are similar or higher at low O_2 concentrations even under conditions such as high irradiance and high CO_2 in which AP would be expected to be insensitive to or stimulated by O_2.

The changes in AP with time after switching O_2 concentrations in Figure 1 may reflect changes in activation of RuBP carboxylase. Sharkey *et al.* (19) have shown that under conditions of TPU limitation in bean, RuBP carboxylase is at a higher state of activation under atmospheric O_2 than at low levels. Changes in AP with time after switching O_2 in Figure 1 are similar to the time required for changes in activation of RuBP carboxylase in wheat leaves after raising or lowering O_2 concentrations (16).

The difference in O_2 response between 84-9 and other *F. linearis* plants is undoubtedly genetic, and possibly results from mutation of some gene or genes coding for enzymes involved in CO_2 metabolism. The variation in O_2 response of AP among the self-pollinated progeny from 84-9 may be genetic variation, but none of the plants had O_2 inhibition approaching that of the other *F. linearis* plants and variability among the replicate measurements of the progeny was high. Further studies of inheritance of this trait will be conducted using hybrids between 84-9 and other *F. linearis* plants as well as other *Flaveria* species.

The significance of occurrence of a plant with O_2 stimulation of AP in a species with C_3-C_4 photosynthesis is not known. Perhaps it is an extreme case of the reduced O_2 inhibition usually observed in C_3-C_4 species and the mechanism for reducing O_2 sensitivity may be common for 84-9 and other C_3-C_4 plants. Except for two experiments, one each with species of *Panicum* and *Flaveria* (13, 14) AP has not been examined in plants of this photosynthetic type at CO_2 concentrations above atmospheric. In both of these studies, however, AP was inhibited by O_2 in the C_3-C_4 species at the highest CO_2 levels used (about 400 μl L^{-1} c_i). In C_3-C_4 *Flaveria* species the inhibition of AP at 350 μl L^{-1} c_i appeared to be greater than in the C_3 species, *Lycopersicon esculentum* (13). So, if O_2 response of AP in the plant 84-9 results from the same mechanism as the reduced O_2 inhibition of AP in other C_3-C_4 plants, it is quantitatively a substantially different response.

The mechanism of O_2 stimulation of AP is still far from clear, as are its implications under physiological conditions. The plant described in this report should be a valuable one for study of O_2 sensitivity of AP since O_2 stimulates AP under temperature, light, CO_2, and O_2 conditions commonly encountered in nature.

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