Carbon Dioxide Exchange Processes in Jojoba (*Simmondsia chinensis*)

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Introduction

All carbon molecules present in living cells of plants are ultimately derived from CO_2 assimilated in photosynthesis. Photosynthesis is a process occurring in the chloroplasts of green tissues of plants, where light energy is converted to chemical energy and used to "trap" CO_2 from the atmosphere and reduce it to carbohydrates.

Not all CO_2 fixed by photosynthesis remains in plant tissues indefinitely. A considerable portion of carbon compounds are broken down and oxidized by respiratory processes, which releases CO_2 into the atmosphere. Two main respiratory processes are recognized, dark respiration (DR) and light respiration (LR). Dark respiration occurs day and night in the mitochondria of all living cells, producing ATP (energy carrier used to drive biochemical reactions), carbon metabolites and CO_2. From 29 to 71% of total CO_2 fixed in photosynthesis can be respired away in dark respiration. Light respiration occurs only in green tissue of plants with the C_3-photosynthetic pathway. This process does not necessarily produce ATP and has been generally considered as a wasteful process.

Plant growth and eventually yields are dependent on carbon gain. A plant shows a positive carbon gain as long as the total CO_2 fixed by gross photosynthesis (GP) exceeds respiratory losses (DR & LR). This net carbon gain is referred to as apparent photosynthesis (AP). So, we have AP=GP-(DR+LR). These components of AP are controlled by environmental conditions and the genetic makeup of the plant.

Jojoba (*Simmondsia chinensis* (Link) Schneider) is a dioecious desert shrub native of the Sonora Desert of the southwestern U.S. Its seeds produce a liquid wax which can be a substitute to whale sperm oil in many industrial processes (Al-Ani et al., 1972; Yermanos, 1974). Jojoba responds well to cultural practices and it has appeared in recent years to be a promising crop for semi-arid regions of the world (Gentry, 1958; Yermanos, 1974).

Jojoba plants growing in the wild present great genetic variability. Al-Ani, Strain & Mooney (1972) suggested that jojoba is differentiated into populations, or ecological races, adapted to the specific environmental conditions of their habitats. Cross pollination among plants within a population further ensures a wide genetic diversity. Zelich (1975) suggested that the photosynthetic and respiratory capabilities of a plant are at least in part genetically controlled. He reported that varieties of corn (*Zea mays* L.) had rates of apparent photosynthesis which ranged from 28 to 85 mg $CO_2 dm^{-2} hr^{-1}$, and a mutant strain of tobacco (*Nicotiana tabacum* L.) had been found with much lower rates of light respiration and higher dry matter production (Zelich, 1975). It is possible that some jojoba populations or individual plants growing in the wild might have developed more efficient photosynthetic and respiratory systems. Plants with higher rates of CO_2 fixation, or lower rates of CO_2 evolution in the light, or greater resistance to water stress could be capable of higher yields (Zelich, 1971, 1975). Jojoba plants grown in controlled environments had rates of apparent photosynthesis around 6.0 $mgCO_2 dm^{-2} hr^{-1}$ (Bunce and Miller, 1976; Collatz, 1977). This is lower than most C_3 plants that usually have rates of CO_2 fixation from 10 to 30 $mgCO_2 dm^{-2} hr^{-1}$ (Zelich, 1971). Rates of light respiration and dark respiration were found to be 3.2 and 1.8 $mgCO_2 dm^{-2} hr^{-1}$, respectively, for plants grown in the greenhouse (Bunce and Miller, 1974).

Jojoba is a true xerophyte which can fix CO_2 at very low levels of leaf water potential (LWP) (Adams et al., 1977; Al-Ani et al.,

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Table 1. Rates of CO_2 exchange processes of 3-month old seedlings originated from 3 different ecotypes.

	Apparent Photosynthesis	Dark Respiration	Light Respiration	Gross Photosynthesis
		$mgCo_2dm^{-2}hr^{-1}$		
Seedlings from	8.9	1.5	9.3	19.8
seeds collected at	8.8	1.9	7.4	18.1
Palomas Plains	7.1	1.7	5.0	13.8
1500 feet elevation	6.7	1.6	7.1	15.4
	3.8	1.7	4.7	10.2
Mean	7.1	1.7	6.7	15.5
Seedlings from	9.4	1.5	5.8	16.7
seeds collected at	7.8	2.5	7.8	18.1
Pima Canyon	7.1	1.3	3.4	11.8
2500 feet elevation	6.5	1.8	6.7	14.9
	5.9	1.6	4.7	12.1
Mean	7.3	1.7	5.7	14.7
Seedlings from	5.9	1.6	3.7	11.2
seeds collected at	5.5	1.5	3.7	10.7
Hot Springs Canyon	5.3	1.6	3.4	10.2
3000 feet elevation	5.2	1.9	4.2	11.3
	5.0	1.4	2.3	8.8
Mean	5.4	1.6	3.5	10.4

1972; Bunce, 1977). Adams et al. (1977) found coastal plants with high rates of CO_2 uptake at LWP of -42 bars. Bunce and Miller (1976) reported that jojoba plants still maintained maximum CO_2 uptake at LWP of -25 bars. Results of Al-Ani et al. (1972) and Bunce et al. (1976) suggest that dark respiration decreases with increasing water stress. Bunce et al. (1976) also reported a decrease in apparent photosynthesis and increase in light respiration with decreasing LWP. Collatz (1977) on the other hand found a linear decrease in apparent photosynthesis and light respiration when jojoba plants were subjected to water stress.

This study was initiated to (a) determine the rate of apparent photosynthesis, light respiration and dark respiration of jojoba plants from three ecotypes, (b) determine the variation in these physiological processes among plants within each ecotype and (c) determine the effect of water stress on physiological processes associated with carbon dioxide exchange.

Materials and Methods

Jojoba seedlings established from seeds collected at Palomas Plains (1500 ft. elevation), Pima Canyon (2000 ft.) and Hot Spring Canyon (3000 ft.) were used in these experiments. Seeds were germinated in 30×8 cm plastic pots in the greenhouse. Soil mix was 50% sandy loam, 25% organic matter (ground bark), and 25% of a 50-50 perlite and vermiculite mixture. Temperature in the greenhouse was 30 C during the day and 20 C at night. Seeds were watered every day until germination and every other day after establishment. Seven-months old seedlings originated from four other localities were used for the water stress measurements. Those seedlings were grown in the same type of pot, soil and water regime, outside the greenhouse.

Apparent photosynthesis, post-illumination burst and dark respiration were measured. From those three parameters light respiration and gross photosynthesis were estimated. Carbon dioxide flux was measured with a Beckman Infrared gas analyzer model 865 in a closed system. Procedures were similar to those described by Foutz, Wilhelm and Dobrenz (1974). Plants were measured at a temperature of 27 C. Illumination at the top of the plant at the time of measurement was 2000 $\mu E\ cm^{-2}sec^{-1}$. Leaf area was obtained with a Hayaski Denko Automatic Area Meter Model No. AAM-5. A Scholander Pressure bomb was used to evaluate leaf water potential.

Five seedlings from each ecotype were measured 3 months after germination to establish the variation in rates among and within the populations. Two seedlings from each population were measured every two hours from 9:00 a.m. to 5:00 p.m. to find the daily fluctuations of CO_2 exchange. For the water stress measurements, all seedlings were brought to field capacity the night before the first measurement and no water was added after that time. Ten seedlings picked at random were tested for CO_2 exchange for seven consecutive days. At each day of measurement five other seedlings, randomly chosen, were used to estimate an average leaf water potential.

Results and Discussion

Jojoba plants displayed tremendous variation in rates of apparent photosynthesis (AP), and light respiration (LR) throughout this experiment. Rates of CO_2 exchange processes of 15 seedlings from 3 different populations grown in a common environment are presented in Table 1. For two of the populations, the variation in rates among plants of the same ecotype was much greater than the differences between their average values. Plants from Palomas Plains had rates of AP that ranged from 7.9 to 3.8 $mgCO_2dm^{-2}hr^{-1}$. Plants from Pima Canyon had rates of LR from 7.8 to 3.4 mg $CO_2dm^{-2}hr^{-1}$. Plants from Hot Spring Canyon, on the other hand, had much less variability in rates of CO_2 exchange. Those plants which originated from the highest elevation had the lowest average value of AP (5.4 $mgCO_2dm^{-2}hr^{-1}$), and consequently the lowest average rate of light respiration (3.5 $mgCO_2dm^{-2}hr^{-1}$). Plants from Pima Canyon and Palomas Plains which had considerably higher rates of CO_2 uptake (7.3 and 7.1 $mgCO_2dm^{-2}hr^{-1}$, respectively) also displayed higher light respiration rates. Dark respiration was very similar for the three ecotypes, averaging 1.7 $mgCO_2dm^{-2}hr^{-1}$. This value is essentially the same as the 1.8 $mgCO_2dm^{-2}hr^{-1}$ reported by Bunce and Miller (1974).

Variation in CO_2 exchange rates was also observed when five plants were measured at different times of the day (Fig. 1). Apparent photosynthesis reached a peak of 10.6 $mgCO_2din^{-2}hr^{-1}$

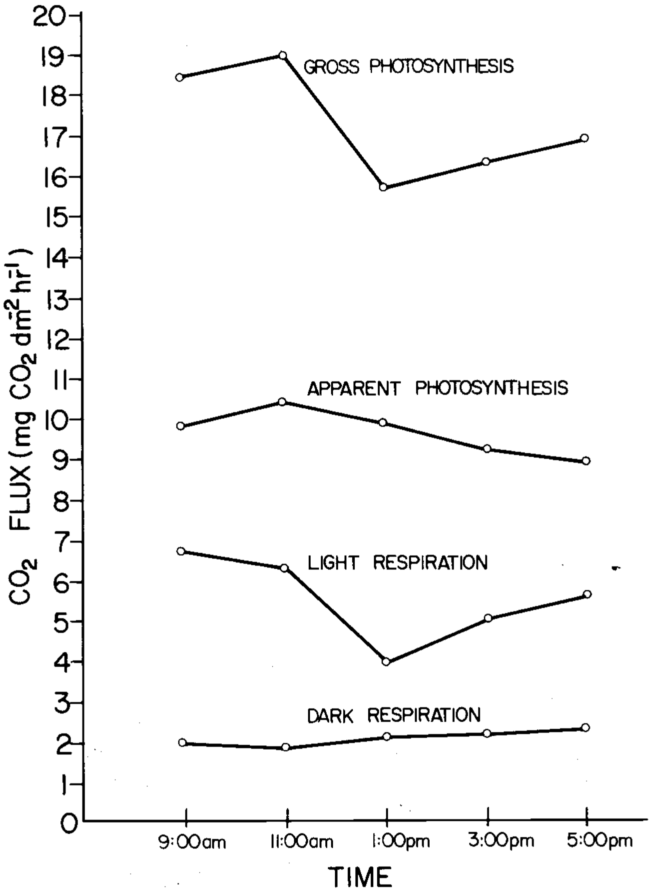

Figure 1. *Average changes in carbon dioxide exchange processes during the day.*

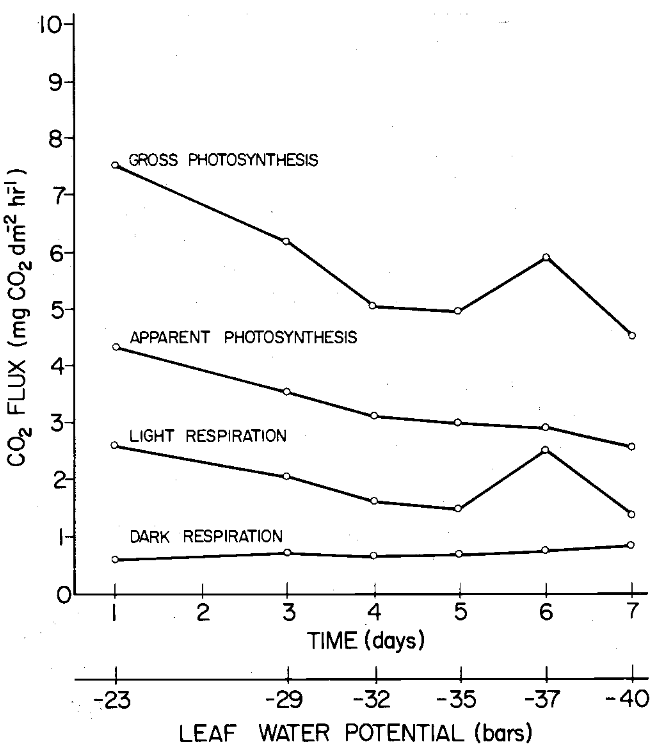

Figure 2. *Average change in carbon dioxide exchange processes and leaf water potential of Jojoba plants measured on seven consecutive days after water application.*

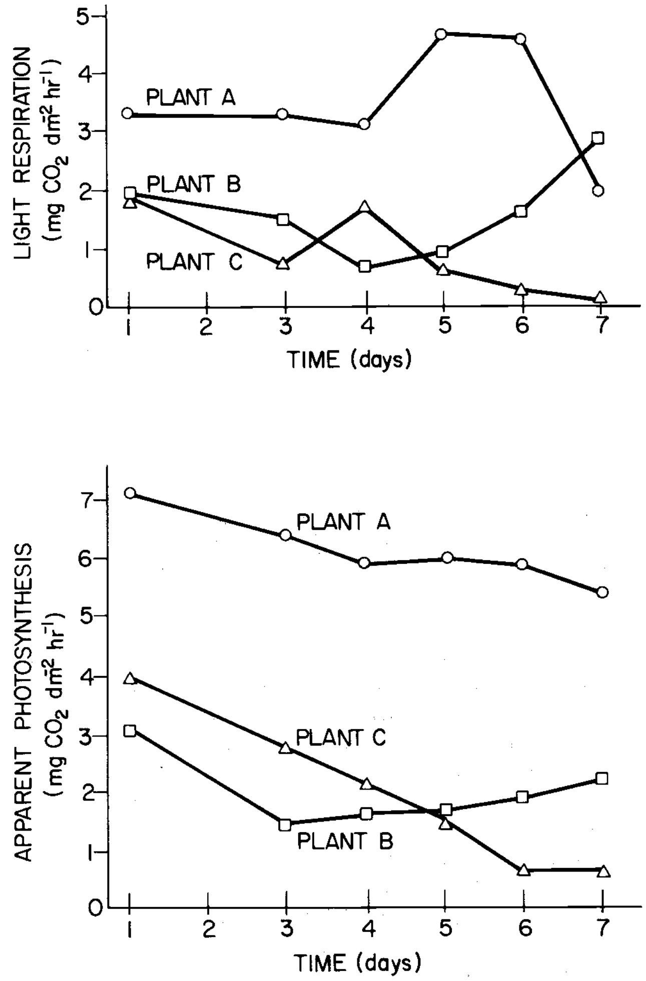

Figure 3. *Variability in apparant photosynthesis and light respiration of three Jojoba clones measured on seven consecutive days after water application.*

at 11:00 a.m., and then decreased gradually by the end of the afternoon. Light respiration and gross photosynthesis were highest in the morning, dropped to their lowest values at 1:00 p.m., and then increased in the afternoon. These marked reductions in rates of light respiration and gross photosynthesis at 1:00 p.m. were undoubtedly caused by midday stomatal closure. Dark respiration remained quite constant throughout the day, increasing slightly in the afternoon.

The highest average leaf water potential observed (-23 bars) is lower than what many plants can survive (Fig. 2). Jojoba plants still had active CO_2 uptake at a leaf water potential (LWP) of -40 bars. This ability of jojoba plants to photosynthesize at very low levels of LWP has already been reported by other authors (Adams et al., 1977; Al-Ani et al., 1972; Bunce and Miller, 1976; Collatz, 1977). Apparent photosynthesis showed a steady linear decrease with decreasing leaf water potential from -23 bars. These results agree with those of Bunce (1977) and Collatz (1977) who found mesophyll and stomatal resistances to increase rapidly only at leaf water potential lower than -20 and -22 bars, respectively. Dark respiration remained unchanged during the seven days of water stress. Average rates of light respiration decreased during the first days, increased abruptly in the sixth day, and dropped to its lowest value on the 7th day.

The change in LR when jojoba plants are stressed for water is a contradictory point in the literature. Bunce and Miller (1976) found a dramatic increase of light respiration with water stress while Collatz (1977) reported a decrease in light respiration. It is possible that genetic differences between plants used by the two authors might explain the opposite results. We found that individual jojoba plants responded quite differently when plants were stressed for water (Fig. 3). Plants A and C (Fig. 3) showed a general decrease in light respiration with water stress which is in agreement with the report of Collatz (1977). The increase in light respiration of plant B supports the results of Bunce and Miller (1976). There were also differences in the apparent photosynthesis of these 3 plants grown with water stress. Plant A had a constant, but slow decrease in apparent photosynthesis. Plant C displayed a sharp decrease to a value of 0.1 $mgCO_2dm^{-2}hr^{-1}$ in the seventh day and plant B had an actual increase in apparent photosynthesis with water stress after the third day.

Summary

The results obtained throughout this experiment lead us to the following conclusions: It is very important that jojoba plants be measured at the same time of day if their rates are to be compared. The CO_2 exchange processes in jojoba are not in steady-state and seem to be very sensitive to small changes in environmental conditions. Light respiration was the most variable CO_2 exchange process while dark respiration was consistently the most stable. Even though the average rate of apparent photosynthesis was lower than for most C_3 plants, jojoba plants were able to take up CO_2 at levels of leaf water potential that would desicate most mesophytic plants. Finally, it was demonstrated that genetic variability for photosynthetic and respiratory processes occurs in jojoba and individual plants responded differently to water stress.

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