A Physiological Study of Developing Pods and Leaves of Honey Mesquite

R. T. WILSON, D. R. KRIEG, AND B. E. DAHL

Highlight: *Photosynthetic and respiratory rates of developing pods and fully expanded leaves of mesquite were assayed during 1972 to determine whether current photosynthesis was sufficient to supply the demands of the developing pods or whether reserve carbohydrates from the roots were required. Net photosynthetic rates of developing pods were very low when expressed as a function of dry weight, whereas the rates of CO_2 evolution were high, suggesting a very active metabolic rate. Leaf photosynthetic rates were comparable to reported rates for other tree species. From the data collected, it was concluded that current photosynthate could not supply the amount of organic matter needed for pod development on trees possessing heavy fruiting loads, and reserve carbohydrates would be needed during the period of maximum rate of dry matter accumulation by the pods.*

Mesquite trees in various phenological conditions respond erratically to foliar-applied herbicides such as the phenoxy acids (Tschirley and Hull, 1958; Fisher, Meadors and Behrens, 1956). These particular herbicides are known to be translocated in the assimilate stream of the phloem (Baidiei, Basler and Santelmann, 1966; Leonard and Crafts, 1956). Therefore, the photosynthate must be actively moving downward in order for sufficient herbicide to reach the root meristems to result in total plant death (Fisher et al., 1956; Dahl et al., 1971).

Recent studies by Wilson (R. T. Wilson, unpublished MS thesis, 1972) suggested that mesquite trees possessing many elongating or maturing pods had a lower concentration of total available carbohydrates in the roots than did trees with relatively few or no pods. Whether the root carbohydrates were translocated upward for pod production or whether the decrease in concentration was due to some other factor, was not determined. Previous work, however, indicates that tree species depend on stored carbohydrates to varying degrees for fruit

production. Kramer and Kowzlowski (1960) stated that during the production of a heavy fruit crop most current photosynthate plus some reserve carbohydrates were used in fruit production.

The primary objective of this study was to determine whether current photosynthate was sufficient to supply the demands of developing pods or whether reserve carbohydrates were needed for pod development. This would allow an estimate of the direction of carbohydrate movement during certain stages of development and possibly offer an explanation for the erratic results often obtained with foliar-applied herbicides.

Materials and Methods

Developing pods and leaves were collected from four mesquite trees (*Prosopis glandulosa* var. *glandulosa*) between May 22 and July 8, 1972. The first sampling, on May 22, was 1 week after miniature pods were first noticed. At the start of the sampling period, 20 to 25 pods were sampled per tree. As the pods aged, only 10 to 15 pods were sampled per tree. Pod length, surface area, and fresh and dry weight determinations were made as a measure of pod growth. Detached leaf and pod samples were assayed for CO_2 exchange properties in a closed system using an infrared CO_2 analyzer. The samples were arranged in a water-jacketed acrylic chamber in a manner approximating the natural position on a tree. The peduncles of the pods and petioles of the leaves were submersed in water to reduce

the rate of dehydration during analyses. Light was provided by an iodine vapor lamp producing 0.7 cal cm^{-2} min^{-1} of photosynthetically active light (400-700 nm) at sample height. The temperature was maintained at 30± 1°C during the light and 25± 1°C during the dark. Net photosynthetic rates were calculated from the time required to reduce the CO_2 concentration within the system. Dark respiration rates were calculated from the time required to replenish the CO_2 concentration within the system.

Results and Discussion

Miniature pods are usually first noticed about the time the leaves are full size and leaf color has changed from light to dark green. In the study area, the tiny pods were first observed on May 15, 1972, 1 week prior to the first sampling date. Pod development proceeded very rapidly, as indicated by the length and weight measurements (Table 1). Within 2 weeks of appearance, pods reached a maximum length of greater than 16 cm. The dry matter accumulation was also very rapid, with the greatest rate of accumulation occurring between the first and second week. Six weeks after appearance, the pods had essentially attained physiological maturity, as indicated by dry matter accumulation. Pod development was observed to occur in the following manner:

a) at 2 weeks of age, small indentations and small seeds were observed;

b) at 3 weeks of age, indentations were more pronounced and seeds appeared as small bumps;

c) at 5 weeks of age, seeds were clearly visible;

d) at 6 weeks of age, pods were turning a pale green and some purple color began to show, (probably indicative of physiological maturity); and

e) at 7 weeks of age, pods were purple-colored and evidently mature.

It was apparent that the growth of the pods was very rapid, and possibly current photosynthate was not adequate to fill the developing pods. This means that carbohydrate reserves had to be translocated from stored reserves to supply the demand of the pods.

Since pods are green, they may significantly contribute to their own development through photosynthesis. In order to test this hypothesis, net photosynthetic rates (mg CO_2/g DW-hr) were determined. The data are expressed as a function of dry weight rather than sur-

Table 1. Growth and CO_2 exchange of developing pods of honey mesquite.

Growth response of pods	Weeks after miniature pods were first noticed						
	1	2	3	4	5	6	7
Dry weight of pods (g DW/pod)	0.11	0.63	0.88	–	1.16	1.18	1.38
Length of pods (cm)	10.70	16.20	16.40	–	–	–	–
Surface area (dm^2/g DW)	0.28	0.13	0.10	–	0.08	0.07	0.06
Net photosynthesis* (mg CO_2/g DW-hr)	0.09	0.03	0.03	–	0.06	0.04	0.02
Dark respiration (mg CO_2/g DW-hr)	4.58	2.09	1.46	–	0.66	0.68	0.54

*Number of samples/mean ranged from two for week seven to seven for week five. All other weeks either four or five samples were analyzed/mean.

Table 3. Apparent photosynthetic and respiration rates of honey mesquite leaves sampled for 2 weeks after the appearance of miniature pods.

	Weeks after miniature pod appearance*	
	4 samples from 4 trees	3 samples from 3 trees
Net photosynthesis (mg CO_2/dm^2-hr)	3.7±1.6	2.3±0.2
Respiration (mg CO_2/dm^2-hr)	1.8±0.3	2.5±0.1

*Mean ± 1 standard deviations.

face area, because as seed size increased the surface area also increased due to undulation, but we could not measure this increase. The results obtained (Table 1) suggest that immature, green pods had a very low net photosynthetic rate. The apparent reason for the low rate of net photosynthesis was the extremely high rate of respiration. The CO_2 compensation points ranged from 245 to 440 ppm (μ l/l) suggesting that under natural conditions (320 ppm CO_2) there was limited net photosynthesis within the pods. No attempt was made to determine the presence or extent of photorespiration within the pod material. By chance, it was noted that pod samples assayed for photosynthetic activity in the afternnoon exhibited a greater net photosynthetic rate than those analyzed in the morning. In order to determine whether the time of day effect was real, pods from the same tree at approximately the same stage of development were analyzed over a 3-week period from June 8 to June 27, 1972. The net photosynthetic rate of the pods was 2 to 4 times greater in the afternoon than in the morning (Table 2). The difference can be attributed to a reduction in the respiration rate of the pods in the afternoon, which increases net fixation of CO_2. Water relations evidently were not improved, because estimates of water concentration (fresh weight/dry weight) were lower in afternoon than in the morning. No reason for the reduction in the afternoon respiration rate is apparent at present. From the results obtained, it is apparent that less than 1 hour of respiration in the dark would deplete the net amount of photosynthate produced during the entire light period of a typical day. Therefore, organic material for pod development must be imported, either from the leaves or from reserve carbohydrates.

Leaf photosynthetic rates were determined to ascertain their potential contribution to pod development. The rates of photosynthesis and respiration (Table 3) obtained for mesquite leaves in this study compare favorably to those reported for other tree species (Zelitch, 1972). A quick calculation would indicate that for the 8-day period beginning May 22, 1972, leaf and pod photosynthesis could not supply all growth demands of the pods. Net CO_2 fixed by leaves and pods for a 14-hour light period on May 23, 1972, was calculated to be 56 mg dm^{-2}. For a 10-hour dark period, the same material would have evolved 165 mg dm^{-2} of CO_2 due to respiration. Therefore, a total leaf area three times the total pod area would have been required just to supply material for respiration, not including growth. However, during the same 8-day period, the pods increased in dry weight about six-fold, from 0.11 g/pod to 0.63 g/pod.

It is apparent that trees possessing heavy fruiting loads are not capable of manufacturing sufficient photosynthate during the period of rapid pod develop-

ment, thus reserve carbohydrates must be called upon to meet growth demands. These data suggest that for mesquite trees with relatively high reproductive potential i.e., large numbers of developing pods, growth-regulating herbicides moving in the assimilate stream probably are not translocated to the root system because the direction of carbohydrate movement would be from the roots to the pods. Current photosynthate produced by trees with few pods would probably exceed that needed for pod development, and recharge of root reserves could occur simultaneously with pod growth. These results should help explain some of the erratic results obtained with foliar-applied herbicides in stands of mesquite containing trees at a given phenological stage but bearing various reproductive loads.

Literature Cited

Baidiei, A. A., E. Basler, and P. W. Santelmann. 1966. Aspects of movement of 2,4,5-T to blackjack oak. Weeds. 14:302-305.

Crafts, A. S. 1956. Translocation of herbicide. I. The mechanism of translocation. Methods of study ^{14}C labeled 2,4-D. Hilgardia. 26:287-334.

Dahl, B. E., R. B. Wadley, M. R. George, and J. L. Talbot. 1971. Influence of site on mesquite mortality from 2,4,5-T. J. Range Manage. 24:210-215.

Fisher, C. E., C. H. Meadors, and R. Behrens. 1956. Some factors that influence the effectiveness of 2,4,5-trichlorophenoxyacetic acid in killing mesquite. Weeds. 4:139-147.

Kramer, P. J., and T. T. Kozlowski. 1960. Physiology of trees. McGraw-Hill Book Co., New York. 642 p.

Leonard, O. A., and A. S. Crafts. 1956. Translocation of herbicides. III. Uptake and distribution of radioactive 2,4-D by brush species. Hilgardia. 26:366-415.

Tschirley, F. H., and H. M. Hull. 1959. Susceptibility of velvet mesquite to an amine and ester of 2,4,5-T as related to various biological and meterological factors. Weeds. 7:427-435.

Zelitch. J. 1971. Photosynthesis, photorespiration and plant productivity. Academic Press, New York. 345 p.

Table 2. A comparison of the morning and afternoon photosynthetic and respiratory rates of honey mesquite pods.*

Time of day and measurement	June 8	June 9	June 20	June 24	June 27	Mean
Net photosynthesis (mg CO_2/g DW-hr)						
Morning rate	0.00	0.02	0.05	0.03	0.02	0.02
Afternoon rate	0.06	0.07	0.08	0.07	0.06	0.07
Dark respiration (mg CO_2/g DW-hr)						
Morning rate	1.72	1.24	0.99	0.62	0.67	1.04
Afternoon rate	1.49	1.38	0.62	0.60	0.57	0.93

*Only dates during study when comparison of morning and afternoon rates were made.