CARBON BALANCE OF *PANICUM COLORATUM* DURING DROUGHT AND NON-DROUGHT IN THE NORTHERN CHIHUAHUAN DESERT

W. B. SISSON

Jornada Experimental Range USDA, Agricultural Research Service, Department of Animal and Range Sciences, New Mexico State University, Las Cruces, New Mexico, U.S.A.

SUMMARY

(1) The daily CO_2 flux of above-ground and below-ground components of *Panicum coloratum* growing in the northern Chihuahuan desert was determined during a spring drought and following the autumn reproductive phase of growth. The objectives were (i) to determine the whole-plant carbon balance after a fifty-two-day drought when photosynthetic capacity was severely repressed, and (ii) to determine the whole-plant carbon balance during favourable soil–water conditions prevalent after the autumn reproductive period.

(2) Water stress severely repressed diurnal photosynthetic capacity during drought. The below-ground biomass, however, consisted of suberized roots with low respiratory activity. The net result was a positive whole-plant carbon gain of 2·6 mg C g dry wt^{-1} day^{-1}.

(3) Precipitation, amounting to 1·12 cm, ended the fifty-two-day drought, and increased the whole-plant carbon gain approximately six-fold.

(4) The mean root/shoot quotient was 1·9 during the spring drought and 0·6 in the autumn. Reproductive tissue accounted for 13–34% (mean = 22%) of the above-ground biomass in the autumn.

(5) Following reproductive growth, when soil-moisture conditions were favourable, the root system comprised suberized roots, non-suberized nodal roots and other non-suberized roots. Although the last two root types had high respiration rates, their presence in low quantities and low soil temperatures resulted in below-ground respiration approximately equal to that during drought. The whole-plant carbon gain during September was 17·2 mg C g dry wt^{-1} day^{-1}.

INTRODUCTION

High temperatures, low annual precipitation, and frequent droughts limit the number of plant species able to inhabit desert environments, as well as their productivity and distribution. Although many plants have morphological and physiological adaptations that help them to cope with this environment, high rates of net CO_2 assimilation and growth usually occur during brief periods coincident with favourable moisture and temperature (e.g. Schulze *et al.* 1980; Kemp 1983; Öquist 1983). Reductions in leaf CO_2 uptake rates due to temperature and moisture stress, and the resulting effect on diurnal leaf carbon balance, have been reported for many plants growing in desert environments (Kappen *et al.* 1976; Chabot & Bunce 1979; Schulze *et al.* 1980). Although a positive leaf carbon balance may result when severe reductions in diurnal net CO_2 assimilation rates occur, a negative whole-plant carbon balance is possible when respiratory CO_2 losses of above-ground and below-ground plant components are simultaneously determined (Sisson 1983). The seasonal timing and duration of depressed or negative whole-plant

carbon balance may influence growth habit and timing of phenological events, as can the allocation of stored carbon reserves (Balasko & Smith 1973; Ryle & Powell 1974). This may be particularly applicable to perennial plants of desert habitats where drought frequently occurs during the growing season.

Plants possess root/shoot ratios as high as 9:1 (Rodin & Brazilevich 1967) and 11:1 (Caldwell & Fernandez 1975) in cold deserts, and close to unity in warm deserts (Barbour 1973). The metabolic costs associated with growth, maintenance, and the annual replacement of all (Shaver & Billings 1975) or part (Caldwell & Camp 1974) of these root systems represent significant allocations of carbon. Ledig, Drew & Clark (1976), for example, found that root respiration amounted to 69% of the daily net CO_2 assimilated in *Pinus rigida*. Daily respiration of the below-ground biomass (roots + caudex) of *Yucca elata* in the northern Chihuahuan Desert amounted to 9% of the daily carbon assimilated in February when environmental conditions for C_3 photosynthesis were optimal, and 300% during August when high ambient temperatures severely depressed leaf photosynthesis (Sisson 1983). Similarly, a negative whole-plant carbon balance could occur as a result of reduced photosynthetic capacity during drought unless a simultaneous and proportionate reduction in growth and maintenance respiration takes place. Cessation of root growth (Molymeux & Davies 1983), root turnover (Caldwell & Camp 1974), and root suberization (Passioura 1983) which occurs during soil drying, reduces respiratory carbon losses during drought. Root systems of drought-tolerant desert plants are, therefore, non-static and respond to wet and dry soil by serial phases of growth and pruning of the root system. Although there are many aspects of drought tolerance, a whole-plant net zero carbon flux, or the maintenance of positive carbon balance could increase the probability of survival during extended drought.

Perennial grasses inhabiting the northern Chihuahuan Desert initiate spring growth in April and May (Kemp 1983). Growth to mid-July is primarily dependent upon soil moisture stored the previous autumn and winter because little precipitation normally occurs during the spring and early summer (2·6 cm total for April–June is the fifty-two-year average). Thus, grasses are typically water-stressed during June when air temperatures often exceed 40 °C. During 1981, no precipitation occurred for fifty-two days before 1·12 cm of rain fell on 24 June. The present study assesses the effect of severe water stress on the daily whole-plant carbon balance of *Panicum coloratum* L., a C_4 perennial bunchgrass. Similar analyses of the whole-plant CO_2 flux were made two days after the rain on 24 June, and in September following reproductive growth. Ambient air temperatures in September were cooler and precipitation, during the thirty days prior to analysis, totalled 5·46 cm.

METHODS

The study was conducted in June and September 1981 on mature *P. coloratum* plants growing on the Jornada Experimental Range (approximately 32°34′N, 104°48′W) near Las Cruces, New Mexico, U.S.A. The plants were grown from seed within an experimental plot established in 1975. Plot soil textures vary from loamy sand to fine sandy loam (Wink series). Average annual precipitation on the study site is 22·1 cm, with 1·2 cm occurring in June and 3·5 cm in September. There was no precipitation for the fifty-

two days before the study began on 23 June; 1·12 cm of rain fell two days before the 26 June analysis and 5·46 cm during the thirty-day period before the final analysis on 10 September.

Net photosynthesis and dark respiration rates of individual leaf blades (held horizontally) and leaf sheaths plus stem (maintained at natural angles) were measured with an open gas circulation system (Sisson 1981). Air temperatures within the cuvette were controlled to $\pm 2\cdot4$ °C of ambient air temperatures. A Beckman model 365 infra-red gas analyser measured differential CO_2 concentrations. Photosynthetically active radiation (PAR; 400–700 mm) was measured with a LI-COR, Inc. Model LI-190SR quantum sensor. Temperatures were measured with fine-wire (copper–constantan) thermocouples.

Respiratory activity of the non-suberized nodal roots, other roots that appeared non-suberized, and suberized roots was determined in September 1981. The non-suberized nodal roots are defined as large, white, rapidly growing, non-suberized perennial roots initiated from root crowns in late August and early September following precipitation. The non-suberized roots are defined as all non-suberized adventitious roots except nodal roots. Suberized roots are all adventitious roots that were suberized (root morphology terminology of Troughton 1957). Because neither non-suberized nodal roots nor non-suberized roots were present on several of the plant root systems excavated in June, only those roots that appeared completely suberized were assessed for respiratory activity during June.

Respiration rates were determined on terminal 6–10-cm portions of intact non-suberized roots. Terminal 6–10-cm portions of non-suberized nodal roots, with or without the terminal growing point, were analysed for temperature-dependent respiratory activity in September. A 6–10-cm portion of suberized roots, approximately 5–15 cm from the root crown, was utilized for respiratory determinations. The non-suberized roots were mycorrhizal, as determined by the method of Bevege (1968).

Individual roots on the south side of plants at a depth of 15–40 cm were located by removing soil until the terminal portions (non-suberized nodal and non-suberized roots) or entire (suberized roots) intact root was exposed. The root was examined to ensure that it was not damaged and was attached to the plant. The root was rinsed with water, blotted dry and sealed into a 6-ml polyurethane cuvette equipped with inlet and outlet ports. The cuvette, containing the root attached to the root system of the plant, was covered with approximately 20 cm of soil. Respiration rates of intact, attached roots were measured with a root gas-exchange system (Sisson 1983). A Gow-Mac Co. Model 550 gas chromatograph with a thermal conductivity detector (60 °C) and poropak Q column (50 °C) measured cuvette CO_2 concentrations before and after each 20 or 30 min incubation period.

Ambient soil temperature fluctuations dictated root temperatures within the cuvette during the first daily root respiration measurement period in both June and September. Thereafter, root temperatures during replicate respiration assays in June and September were controlled to within $\pm 1\cdot4$ °C of these initial diel root temperatures by a watercooled peltier thermoelectric stage (Cambridge, Thermionic Corp., Cambridge, Massachusetts, U.S.A.) mounted on an aluminium heat exchanger into which the cuvette was inserted.

Respiratory activity of excised root crowns from field-grown plants was measured by manometric techniques (Umbreit, Burris & Stauffer 1964).

Before analysis, soil particles were washed from the root crowns, the cut surfaces sealed with lanolin, and the crowns soaked for 5 min in 20% Chlorox (1 ml Tween 20/1) to minimize the microbial contribution to respiratory gas exchange. Oxygen was measured

directly in microlitres O_2 taken up per minute within a 10-ml reaction vessel at 25 °C (± 2 °C). Cuvette CO_2 was absorbed in 10 M KOH.

Three individual *P. coloratum* plants were destructively sampled in June and five plants in September 1981 to quantify biomass partition of the above-ground and below-ground components. Mature inflorescences were present on the plants extracted in September. An attempt to remove the entire root system of each plant was made by sieving all soil within a radius of approximately 2 m from the base of each plant to a soil depth of 1–2 m. The non-suberized nodal and non-suberized roots were estimated to form approximately 5% and 1% of the root biomass on a dry weight basis in September, respectively. These values, however, are approximate, because extraction of the complete root system was not feasible. Nevertheless, because extreme care was taken during root extraction, the biomass values obtained are assumed to be reasonably accurate.

RESULTS

June CO_2 exchange

The dry soil conditions prevailing on 23 June resulted in predawn and midday (solar noon) mean leaf water potentials of -1.52 and -2.59 MPa, respectively; partial leaf rolling was evident within the canopies of most plants by 08.00 hours. All *P. coloratum* plants showed slight to total leaf roll by solar noon. Although gains in CO_2 occurred throughout the photoperiod, leaf net CO_2 assimilation rates were low (Fig. 1b). Rain (1·12 cm) fell on 24 June and substantially higher leaf net CO_2 assimilation rates were measured on 26 June (Fig. 1b), the first cloudless day following the rain. Pre-dawn and midday mean leaf water potentials on 26 June were -0.90 and -2.04 MPa, respectively, and there was no leaf rolling during the photoperiod. Nevertheless, the progressive decline in net CO_2 assimilation rates through the photoperiod suggested that water stress may have depressed photosynthetic activity. Net CO_2 assimilation rates were similar on 23 and 26 June after 17.00 hours. Diurnal leaf sheath plus stem net CO_2 assimilation rates were essentially identical on 23 and 26 June and were, therefore, combined for Fig. 1b. Thus, the rain of 24 June had little or no measurable effect on the photosynthetic rates of these plant components.

The root biomass of *P. coloratum* plants consisted entirely of suberized roots during June. Daily respiratory activity of these roots was highly temperature-dependent (Fig. 1c): maximum and minimum respiration rates coincided with high and low root temperatures, respectively. These figures result in a Q_{10} of 1·5. Daily root respiration rates were similar on 23 and 26 June and were combined in Fig. 1c.

September CO_2 exchange

Total precipitation on the study site was 5·46 cm during the thirty days before 10 September and air temperatures were low (Fig. 2a). As a result, there were no visible signs of plant water stress (e.g. leaf rolling) or midday depression in net CO_2 assimilation rates (Fig. 2b). Although leaf photosynthetic rates were substantially different in June and September, diurnal leaf sheath plus stem net photosynthetic rates measured in September (Fig. 2b) were similar to those in June (Fig. 1b).

Substantial above-ground and below-ground growth occurred prior to the September analysis. The below-ground biomass consisted of three root types (non-suberized nodal, suberized and non-suberized) in September. Daily fluctuations in respiratory activity of the three root types were a function of temperature while respiration rates were a function
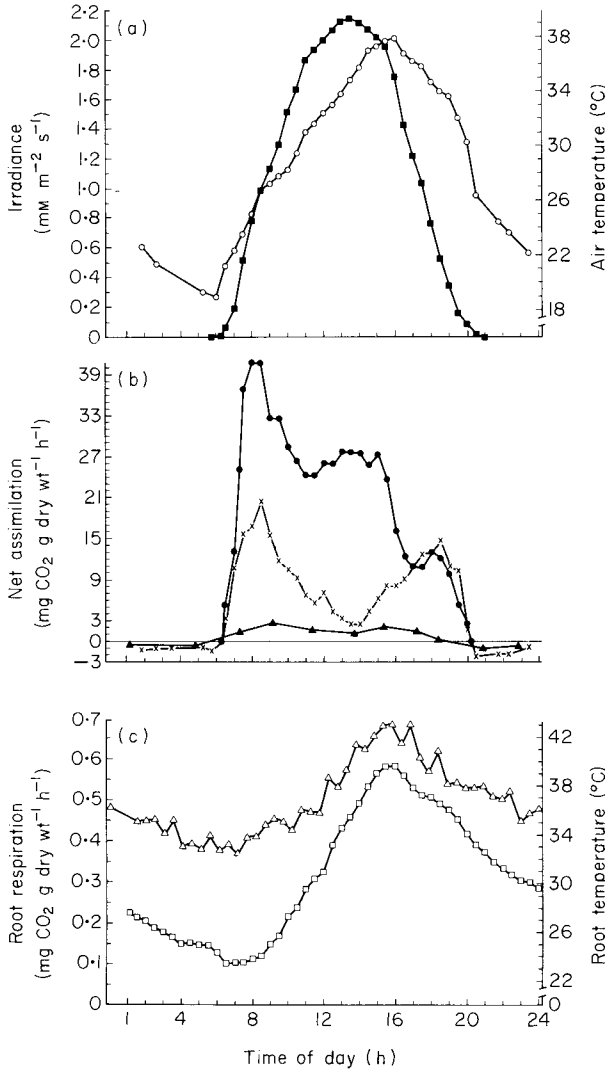
Fig. 1. Photosynthesis and respiration of *Panicum coloratum* on two cloudless days before and after rainfall in the north Chihuahuan Desert, New Mexico. (a) Irradiance (■) and air temperature (O); points represent means of figures recorded on 23 and 26 June 1981; 1·12 cm of rain fell on 24 June. (b) Daily net photosynthesis and dark respiration in a single plant, in leaf blades during 23 June (×) and 26 June (●), and in leaf sheaths and stems (▲) on both days. (c) Mean temperatures (□) and respiration rates (△) of two suberized roots at 20 cm soil depth, determined on 23 and 26 June 1981. Hours are mountain daylight time (MDT + 88 min = mean solar time).

of root type (non-suberized nodal > non-suberized > suberized) (Fig. 3). In September, daily root temperatures at 20 cm soil depth (Fig. 3) were approximately 10 °C lower than those in June (Fig. 1c). Respiration rates of suberized roots in September were 40% and 70% less than those in June when maximum (approximately 17.00 hours) and minimum (approximately 08.00 hours) soil temperatures occurred, respectively. The calculated Q_{10} value for the suberized roots was 4·1 when based on mean respiration rates coincident
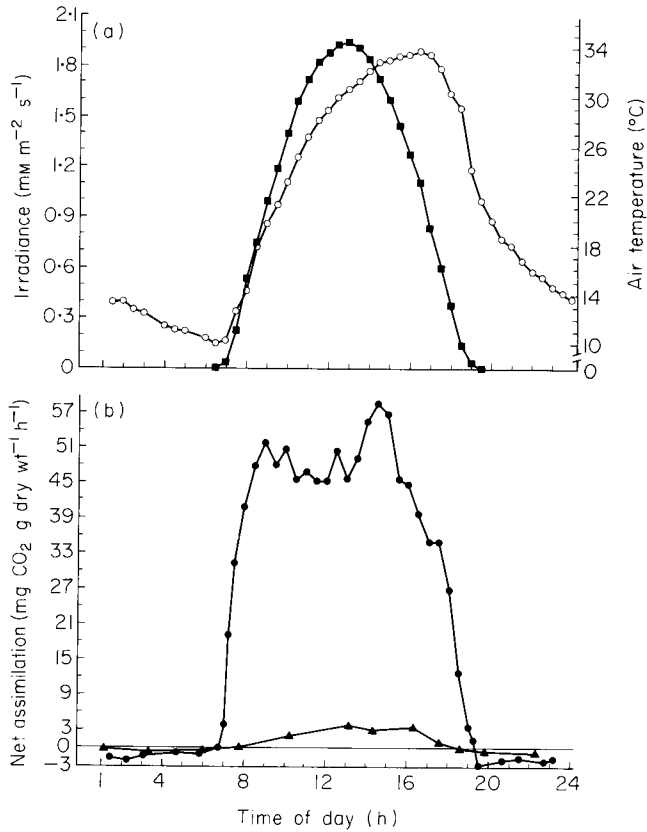
FIG. 2. Irradiance (■) and air temperatures (O), mean net photosynthesis and respiration of leaf blades ($n=2$) (●), and of leaf sheaths plus stems ($n=2$) (▲) of two *Panicum coloratum* plants in the northern Chihuahuan Desert on 10 September 1981. Hours are mountain daylight time (MDT $+88$ min $=$ mean solar time).

with high and low daily root temperatures. Similar values for non-suberized nodal and non-suberized roots were 2·4 and 2·2, respectively.

Respiration rates of the three types of roots, as a function of temperature, are shown in Fig. 4. The above-ground plant components were kept in the dark during the photoperiod to negate any influence of photosynthesis on root respiration. A 6–10-cm portion of the non-suberized nodal roots, immediately behind the terminal growing point and including the terminal growing point (Fig. 4), was used for respiratory measurements. Individual roots were maintained at each temperature (5–40 °C) for approximately 40 min before respiration rates were measured. Respiratory activity attributable to terminal meristematic tissue of non-suberized nodel roots accounted for an average of 31% (range 11–61%) of the total respiration. Calculated Q_{10} values, based on root temperatures of 30 and 40 °C, were below 2·0 for all root types (range 1·4–1·6). Using 10 and 20 °C root temperatures and the associated respiration rates, Q_{10} values were highly variable: 3·4, 2·0, 1·2 and 2·4 for the non-suberized nodal roots excluding and including the terminal growing point, and the suberized and non-suberized roots, respectively.
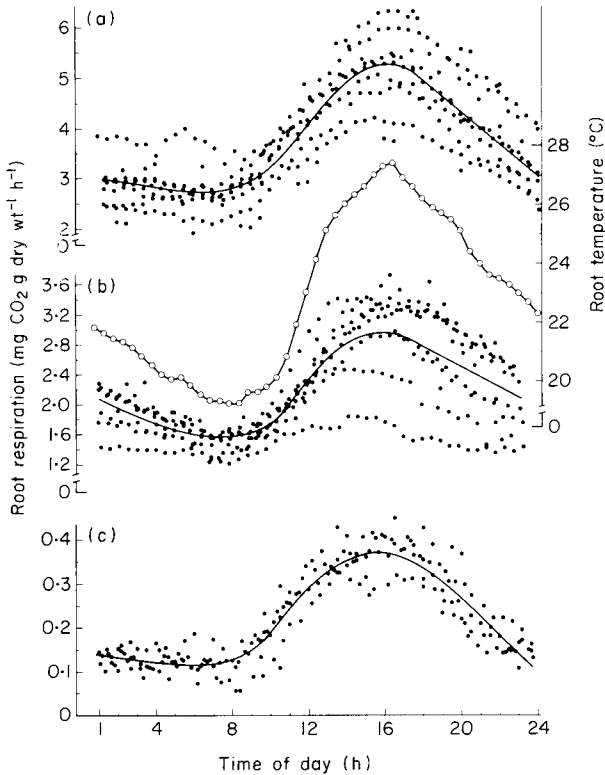
FIG. 3. Daily root temperatures (O) and respiration rates (●) for (a) the non-suberized nodal ($n = 8$), (b) non-suberized ($n = 8$) and (c) suberized ($n = 5$) roots of *Panicum coloratum* at 20 cm soil depth growing *in situ* in the northern Chihuahuan Desert during cloudless days between 2 and 17 September 1981. Each point (●) represents a single respiration rate and the curves are hand-drawn. Standard errors of the mean of all root respiration rates within each hour ranged from 0·11 to 0·21, 0·02 to 0·09 and 0·01 to 0·02 for the non-suberized nodal, non-suberized and suberized roots, respectively. Hours are mountain daylight time (MDT + 88 min = mean solar time).

Biomass analysis

Dry weights of above-ground and below-ground components of eight *P. coloratum* plants removed from the soil are shown in Table 1. Three plants of uniform size were harvested in June and five plants, representing a range of sizes, in September. Because of the sizes of the plants removed, the low numbers of plants harvested, and the difficulty in retrieving the entire below-ground biomass of living roots, root/shoot quotient and root biomass values may not be absolutely correct. Nevertheless, the higher root/shoot ratios of plants harvested in June reflect the absence of new growth because of the dry soil conditions. Plants harvested in September following reproductive growth possessed root/shoot ratios consistently lower than those taken in June. These lower values were the result of considerable above-ground and below-ground growth, resulting from favourable soil moisture conditions before harvest.

Carbon balance

Dry weights of individual plant components (Table 1; plants number 3 and 8) were used to calculate a carbon balance of whole plants during June and September (Fig. 5). Root-
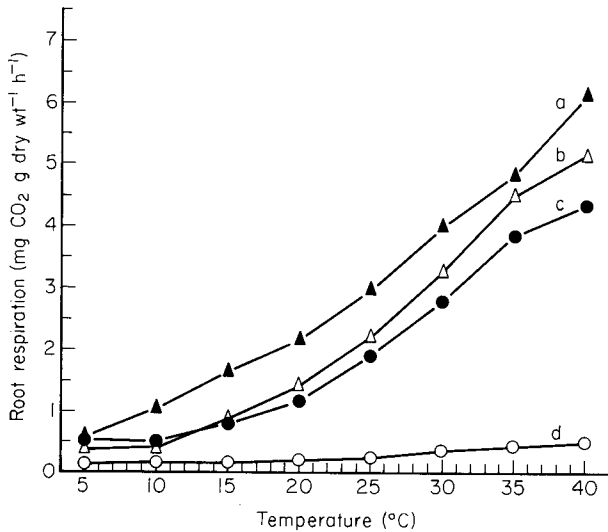
FIG. 4. Response of respiration in intact, attached non-suberized nodal roots including (▲) and excluding (△) the terminal growing point, and non-suberized (●) and suberized (○) roots of *Panicum coloratum* plants during cloudless days in the northern Chihuahuan Desert during September 1981. Standard errors of the means (*n* = 3 or 4) ranged from 0·06 to 0·73.

TABLE 1. Root/shoot quotients and dry weights (g) of the below-ground and above-ground components of eight individual *Panicum coloratum* plants removed from soil in the northern Chihuahuan Desert during June (plants 1–3) and September (plants 4–8) 1981.

	June			September				
Plant number	1	2	3	4	5	6	7	8
Root/shoot quotient	1·6	1·9	2·3	0·4	0·7	0·5	0·5	1·2
Total dry weight (g)	23·3	25·3	25·9	189·6	63·4	24·2	41·2	331·0
Roots	9·8	11·5	14·7	41·1	19·4	6·8	7·9	131·7
Root crown	3·3	3·5	3·4	14·8	7·1	1·3	6·0	47·1
Leaf sheaths + stems	3·5	3·4	2·5	89·1	19·4	9·1	15·3	93·1
Seed head	—	—	—	19·8	9·5	3·4	4·4	17·8
Leaf blades	4·8	4·6	5·3	25·0	8·1	3·5	7·7	41·3

crown respiration rates determined at 25 °C during June and September were 0·152 (±0·014) and 0·198 ± (0·023) mg C g dry wt^{-1} h^{-1}, respectively. These values were used to calculate daily root crown respiration, using a Q_{10} of 2 and the June (Fig. 1c) and September (Fig. 3) root temperatures. A measurable CO_2 flux was absent from the mature inflorences.

A positive carbon balance was present during both June and September. Rain (1·12 cm) on 24 June resulted in a sixfold increase in carbon gained per total plant on 26 June (0·383 g C 25·9 g dry wt^{-1} day^{-1}) relative to the whole-plant carbon gain on 23 June (0·066 g C 25·9 g dry wt^{-1} day^{-1}) (Fig. 5). The whole-plant carbon gain during the cooler month of September, after 5·64 cm of precipitation, was 5·714 g C 331 g dry wt^{-1} day^{-1}. Although total carbon gain per plant was substantially different in September, and on 26 June
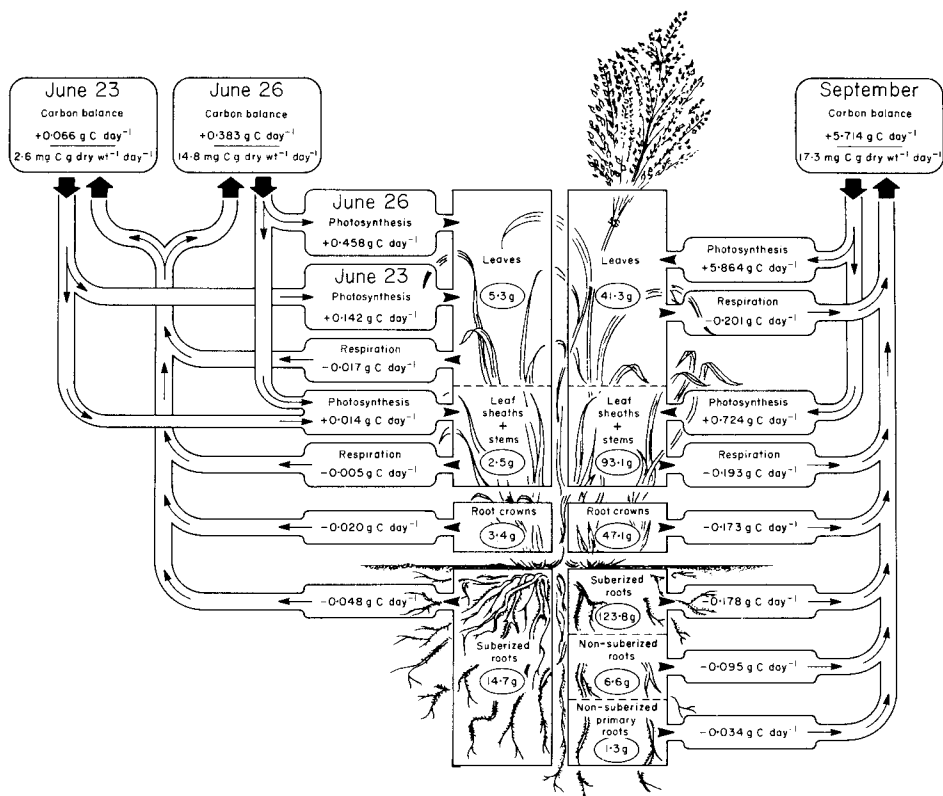
FIG. 5. Carbon balance of *Panicum coloratum* in the northern Chihuahuan Desert during cloudless days in June and September. Values in circles are dry weights for the different components of an individual plant excavated in June and September.

following the 1·12 cm of rain, carbon gained per unit of plant dry weight was similar during these two periods: 17·3 and 14·8 mg C g dry wt^{-1} day^{-1} for September and June, respectively. Carbon gained per unit dry weight on 23 June was considerably lower (2·6 mg C g dry wt^{-1} day^{-1}). Respiration associated with the below-ground biomass was 3·7 and 2·3 mg C g dry wt^{-1} day^{-1} for June and September, respectively.

DISCUSSION

Growth by *Panicum coloratum* during the dry, cool months of April and May was dependent on soil moisture stored the previous autumn and winter. By 23 June, following fifty-two days devoid of precipitation on the study site, severe plant water stress substantially depressed diurnal CO_2 assimilation rates. Considering the high soil temperatures (Fig. 1c), the dependence of root respiratory rates on temperature (Fig. 4), and the high proportion of root biomass relative to shoot biomass (root/shoot = 2·31; Fig. 5), a negative whole-plant carbon balance might have been predicted. However, a low below-ground carbon loss (3·7 mg C g dry wt^{-1} day^{-1}; Figs 1c and 5), because all roots were suberized, coupled with a low but positive above-ground carbon gain (17·3 mg C g dry wt^{-1} day^{-1}), resulted in a positive whole-plant carbon gain (2·6 mg C g dry wt^{-1}

day^{-1}; Fig. 5). In carbon equivalents, this gain in carbon (g C g dry wt^{-1}) is approximately equal to maintenance respiration (Penning de Vries 1972) when adjusted for the effect that water stress has on maintenance respiration (Wilson, van Bavel & McCree 1980). Rain (1·12 cm) on 24 June substantially increased leaf net CO_2 assimilation rates and, consequently, the whole-plant carbon gain (14·8 mg C g dry wt^{-1} day^{-1}; Fig. 5). This amount of carbon is enough to synthesize approximately 23 mg dry wt g dry wt^{-1} or 27 mg CH_2O g dry wt^{-1} above that needed for daily maintenance respiration, using the growth and respiration coefficients of Penning de Vries (1972). The estimated proportion of carbon available for allocation to growth or reserve substrates is probably conservative because maintenance respiration of plants growing in a field situation may be lower than it is in controlled environments (Caldwell & Fernandez 1975; Sisson 1983). Nevertheless, relative to carbon costs, the 1·12 cm of rain changed the calculated whole-plant carbon balance from that which would meet the daily maintenance requirements during drought to one capable of assimilating sufficient carbon for allocation to growth or reserve substrates.

The ability of roots to change from a non-suberized condition, with high growth and maintenance respiration rates (Fig. 4), to a suberized state, with low respiration rates (Fig. 2c) when soil dries (Passioura 1983), considerably reduces carbon costs during drought. Similarly, cessation of root growth, a reduction in total root biomass by root turnover, and a reduction in respiratory capacity conserves carbon when soil-water deficits depress photosynthetic capacity (Dahlman 1968; Caldwell & Camp 1974; Shaver & Billings 1975; Holthausen & Caldwell 1980). During drought, therefore, a relatively large root biomass (root/shoot > 1; Table 1) can be maintained within a large soil volume because of the low respiration costs associated with highly suberized roots. When favourable environmental conditions supported high CO_2 assimilation rates and root growth in September (Fig. 2b), the root respiration component of the whole-plant carbon balance was small (Fig. 5). Respiration of the below-ground biomass in September (2·3 mg C g dry wt^{-1} day^{-1}) was, in fact, approximately equal to that in June (2·6 mg C g dry wt^{-1} day^{-1}) even though non-suberized (Fig. 3b) and non-suberized nodal (Fig. 3a) roots were present in September and had relatively high respiration rates. The small proportion of these two root types and the low daily soil temperatures (Fig. 4) resulted in low below-ground respiratory activity. The net result was that a large proportion of assimilated carbon could be allocated to reproductive, photosynthetic and root tissue and to reserve substrates.

The mean root/shoot quotients of *P. coloratum* were 1·9 in June and 0·6 in September with a composite range of 0·5–2·3. These quotients are within the range of published values for several range grasses (0·18–2·43) (Bray 1963) and plants of various desert communities (cited in Barbour 1973). Disparity in seasonal quotients of *P. coloratum* may have resulted from differential soil moisture available for growth in June and September and, in part, from reproductive growth in September. Reproductive tissue accounted for 13–34% (mean = 22%) of the above-ground biomass in September and 5–15% (mean = 11%) of the whole-plant biomass (Table 1).

Initiation of growth in March and April by *P. coloratum* would be a survival risk if carbon (energy) costs, associated with construction and maintenance of photosynthetic tissue and roots, exceeded reserve substrates and carbon assimilated throughout the typically dry spring and early summer of the northern Chihuahuan Desert. The risk would be somewhat proportional to the level of soil moisture present when growth begins and the total biomass constructed before soil moisture depletion. Because respiration is temperature-dependent and proportional to total biomass, a large increase in plant

biomass prior to drought and the maintenance of this tissue during drought could eventually deplete plant carbon reserves during the dry, hot months of May, June and July when photosynthetic capacity is depressed. The ability of *P. coloratum* to maintain a positive whole-plant carbon balance during extended periods devoid of precipitation negates this effect and suggests that this plant is adapted to the frequent droughts of the northern Chihuahuan Desert during the growing season.

ACKNOWLEDGMENTS

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