Soil Biol. Biochem. Vol. 15, No. 3, pp. 303–309, 1983
Printed in Great Britain.

0038-0717/83/030303-07$03.00/0

SOIL RESPIRATION IN A CHIHUAHUAN DESERT RANGELAND

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(*Accepted* 30 *September* 1982)

Summary—Soil respiration of a desert soil was measured at the New Mexico State University Ranch in Southern New Mexico. Respiration rates were highest during late July and August after summer rains. Soil respiration data were used to estimate soil organic matter turnover which was 54 yr using summer data and 20 yr using both summer and winter data. The long turnover estimate for summer measurements resulted from temperatures above optimum in June and July. Diurnal soil respiration was also measured after a simulated 2.54 cm rain event. For both wetted and dry soils, temperature controlled the patterns of soil respiration with an optimum of near 41°C. Activation energy values decreased from 84.91 to 39.5 kJ mol^{-1} when the soil was wetted. A light–dark container method was tested as a possible means of estimating algal uptake of CO_2, however, the method was not feasible for desert soils.

INTRODUCTION

Total soil respiration is an important ecosystem attribute that provides an estimate of the turnover of soil organic matter. Soil respiration results from the activity of soil microflora, soil animals and roots (Coleman, 1973). Coleman (1973) separated root respiration from soil and animal respiration and found that roots contributed only from 6 to 17% of the total CO_2 evolved from a grassland soil. He suggested that 45% of the root respiration probably resulted from rhizosphere microflora, therefore, only 3–9% was attributable to roots; hence, most of the soil respiration could be attributed to soil microflora and animals. Wiant (1967) and Witkamp and Frank (1969) estimated root respiration as 50% of total soil respiration in forests soils. However, they did not separate root from the rhizosphere microfloral respiration. Soil animals (protozoa, nematodes and arthropods) contribute only a small portion (3–20%) of the total CO_2 output of soils (Nielsen, 1961; Macfadyen, 1971; Edwards and Sollins, 1973) and from decomposing roots and litter in a desert ecosystem (Parker *et al.*, 1983). Soil microbes are thus the major contributors (approximately 71%) to the CO_2 flux from soils.

Wetting of soils stimulates organic matter decomposition and, thus, soil respiration (Birch, 1958; MacGregor, 1972). In deserts, moisture is also a major limiting factor to primary productivity, and therefore, carbon input into soils (Noy Meir, 1973). Soil water potentials in the Chihuahuan desert are less than −3 MPa during most of the year and soil water potentials less than −10 MPa are common. Since moisture is limiting during early summer, a time of high litter decomposition rates (Comanor and Staffeldt, 1978), Whitford *et al.* (1981) have proposed that diurnal fluctuation of soil moisture might allow for periods of biological activity in the early morning hours. Edwards and Sollins (1973) measured diurnal patterns of respiration in forest litter and found highest rates at night. However, Witkamp (1969) demonstrated that diurnal patterns of soil respiration in forest soils was controlled by soil temperature, with the highest rates occurring in the afternoon. So if diurnal respiration is controlled by soil temperature, then the estimation of energies of activation for soil respiration would be useful for comparing ecosystem responses to temperature.

Soil respiration has been measured for all biomes (Singh and Gupta, 1977); however, there are limited data on respiration in desert soils (Rixon, 1971; Comanor and Staffeldt, 1978; Comanor and Freeman, 1978; Parker *et al.*, 1983). In view of the paucity of data on respiration in desert soils, we conducted studies to: (1) measure soil respiration and estimate soil organic matter turnover, (2) measure diurnal soil respiration during midsummer and determine if microbial activity is stimulated in the early morning hours, (3) use diurnal respiration data to estimate energies of activation, (4) measure the effects of simulated rain on the diurnal pattern of litter and soil respiration, (5) attempt to measure algal uptake of CO_2 and (6) measure the relationship between temperature and abiotic soil respiration.

METHODS

The base absorption method was used for the measurement of soil respiration seasonally and the effect of a simulated rain on litter and soil diurnal respiration. These studies were conducted on the desert watershed at the New Mexico State University Experimental Ranch, 40 km NNE of Las Cruces, New Mexico. The soil is an Alladin complex and is an Aridic Entic Haplustoll coarse loam. The dominant cover is creosotebush, *Larrea tridentata*.

The first experiment was a survey of continuous soil respiration under creosotebush canopies during

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the growing season (May–September, 1979). Continuous measurements as opposed to instantaneous measurements were chosen because they measure total CO_2 output from the soil, which is necessary for estimating soil organic carbon turnover. Instantaneous measurements, being time-of-day dependent, can greatly under or over estimate total CO_2 output from soil and are impractical when the study site is 40 km from the laboratory. Further, long term CO_2 measurements allow the soil carbonate pool to equilibrate during wetting and drying processes. In this study, 12.5 cm dia cans open at both ends were forced 10 cm into the soil with a minimum amount of soil disturbance. The cans were placed under the northeast side of the shrub canopy to reduce solar radiation and thus keep thermal loading and condensation at a minimum. The exposed ends were sealed with plastic lids and covered with aluminum foil to further reduce thermal loading and condensation. Carbon dioxide traps (25 ml 1 N NaOH) were replaced weekly with fresh traps. The 25 ml NaOH provided a surface area that was 25% of the soil surface area encompassed by the trap. No more than 30% base neutralization occurred during the study. There were five replicates for each set of measurements. First-order rate constants (k) for carbon mineralization were estimated by the relationships:

$$\log C = mt + b \quad (1)$$

$$k = -2.303\, m \quad (2)$$

where C is the soil carbon (g m^{-2}) remaining; t is time in days; b is the intercept (g m^{-2}); and m is the slope. Carbon disappearance was assumed to be as CO_2. The initial soil organic carbon level was 2086 g C m^{-2} (Barth and Klemmedson, 1978).

The second experiment was a long-term study of soil respiration from June 1981 to January 1982. Screen enclosures (13 cm dia) were used to prevent litter from falling on the soil surface. A total of 15 enclosures were used (three sets of 5 replicates). A rotation was established so that one set of enclosures was used at a time and then not used for two consecutive measurements. The CO_2 traps were replaced twice a week by collecting the old trap and placing the new traps in the next set of enclosures. Cans (10 cm dia) were placed in the CO_2 traps and forced 2 cm into the soil during the measurement and removed after the measurement. This rotation allowed the soil to be exposed to natural conditions for 13–14 days before being covered for either 3 or 4 days during the measurement. Soil moisture potential was measured with thermocouple psychrometers at depths of 5 and 15 cm when every CO_2 trap was changed. Soil temperature was measured at these depths using a continuous recorder.

The third experiment was carried out in July, 1979 to determine the effects of simulated rainfall on the diurnal pattern of soil and litter respiration. Litter was collected from under creosotebushes. The litter was approximately 60% creosotebush leaves with the remaining 40% annual plant parts, rabbit feces, mesquite leaves and parts of grasses. Twenty-five grams of litter was confined in open bottom screen cylinders (9.8 cm dia) to prevent litter from being scattered. These quantities approximate the concentrations of litter normally found under shrubs in the area. The litter in the cylinders was left in the field for 6 days prior to simulated rainfall. The litter was then wetted with the equivalent of 25.4 mm of water. The wetting front in the soil below the litter was expanded to an 18 cm dia circle. Carbon dioxide was measured for a 1 h interval from 0400–0500, 1400–1500, and 2200–2300 h on days 1, 2, 4 and 8 after the simulated rain event. Carbon dioxide was trapped by placing a 9 cm dia can over the litter and forcing the can 1 cm into the soil. Litter respiration was estimated by subtracting soil respiration from the respiration of soil with a litter layer. Soil and litter moisture was determined by the gravimetric method (105°C for 24 h). Soil temperatures were taken by inserting a standard laboratory thermometer into the side of the hole left when soil moisture samples were removed.

In the fourth experiment, we measured soil respiration on the first day after a simulated one inch rain event using an incubation time of 2 h. For this experiment we measured soil respiration under *Larrea tridentata* shrubs and in intershrub areas. Only the under shrub areas were watered. We also used a light–dark container method to determine if CO_2 fixation by soil algae was decreasing soil respiration measurements in wetted soils. The light containers were translucent plastic tubs (14.7 cm dia and 19 cm high) while the dark containers were the same except covered with aluminum foil. Soil temperatures were measured prior to placing the container on the soil surface and immediately after removing the container (2 h later).

Activation energies (E_A) were calculated for soil respiration below the optimum temperature by the following relationship:

$$\ln v = \frac{E_A}{0.474T} + A \quad (3)$$

where v is the respiration rate (mg m^{-2} h^{-1}); T is the temperature (°K); and A is a constant (mgC m^{-2} h^{-1}).

A fifth experiment was conducted to determine the magnitude of abiotic CO_2 fluxes from the soil used in the above studies. Microcosms consisting of 50 ml Erlenmeyer flasks containing 25 g of soil were gamma sterilized. Replicate microcosms were placed in 0.5 l respiration chambers and incubated at temperatures of 4, 22, 45 or 60°C for 24 h. Then enough sterile water was added to bring the soils to field capacity and immediately placed back into the respiration chambers with a CO_2 trap (1 N NaOH) and incubated at their respective temperatures. Every 24 h the traps were replaced with fresh traps.

All data were subjected to analysis of variance. When significance was observed at the $P = 0.05$ level, Tukey's Q-values were calculated for mean separation. Differences between activation energies (E_A) and the constant A were assessed by Student's t-test (Sokal and Rohlf, 1969).

RESULTS AND DISCUSSION

The summer is the time of maximum litter disappearance (Comanor and Staffeldt, 1978). Most of the annual precipitation falls during these months and

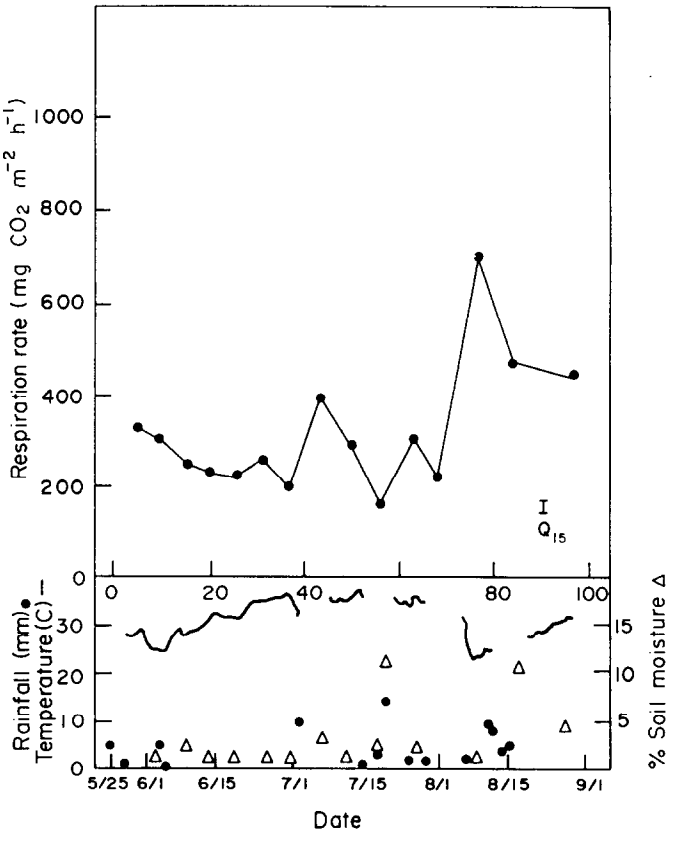

Fig. 1. Rates of carbon mineralization and abiotic factors for a desert soil during the growing season of 1979.

the soil temperatures are high, thus providing the greatest potential for carbon loss (as CO_2) from the system. Soil respiration during the growing season could be separated into a wet (late July and August) and a dry (May, June and the first part of July) period. Soil respiration increased following rain events in July and August but not in June (Fig. 1). Even though rain events occurred in May and June, the wetting front was insufficient to penetrate to the 10 cm depth of the can. Since soils were covered at all times except during the change of CO_2 traps, soil respiration could only respond to either a high intensity rain event or a number of small rain events in close succession so that the wetting front moved below 10 cm. The rates of soil respiration ranged from 167 to 708 mg $CO_2\,m^{-2}\,h^{-1}$ for the growing season and were generally higher than those observed for most forest ecosystems (Singh and Gupta, 1977). The respiration rates were similar to a number of grassland ecosystems (Singh and Gupta, 1977). This is probably a result of the high soil temperatures that are characteristic of grassland and desert ecosystems in comparison to forest ecosystems.

The first-order rate constant for carbon mineralization was $1.53 \times 10^{-4}\,day^{-1}$ for the entire growing season. First-order rate constants for the dry and wet seasons were 1.49×10^{-4} and $1.79 \times 10^{-4}\,day^{-1}$, respectively, which were different ($P = 0.0001$). The half life ($0.693/k$) of soil organic carbon was estimated as 12.54 yr and the turnover ($3/k$) or the time for 95% loss of soil organic as CO_2 was 53.6 yr. This represents a rough estimate of turnover of total soil organic carbon due to the complication that soil organic matter is composed of a number of different fractions varying in their resistance to decomposition (Paul and Van Veen, 1978). This probably overestimated organic matter turnover since it was based on the warmest time of the year, however, this value was similar to the turnover of soil organic carbon (63 yr) estimated time in a New Zealand pasture (O'Brien and Stout 1978). Jenkinson and Rayner (1977) estimated a higher turnover (16–22 yr) of carbon in agricultural soils.

Summer soil respiration was not significantly correlated with any of the abiotic factors measured. The lack of a significant correlation with soil moisture was probably a result of the means of measuring soil moisture. Soil moisture was an instantaneous measurement whereas CO_2 was a weekly average. Therefore, soil moistures at the time of sampling, were sometimes considerably lower than those during the CO_2 measurement. However, the lack of significant correlations could mean a combination of factors was important.

When winter respiration is taken into account a higher K value ($3.976 \times 10^{-4}\,day^{-1}$) and thus shorter half life (4.78 yr) and turnover (20.7 yr) than using just summer respiration data was observed. Respiration was higher in the cool winter months than the hot dry summer months (Fig. 2). Coolest soil temperatures are observed between 1 and 23 January and can occassionally approach 0°C, however, these soils

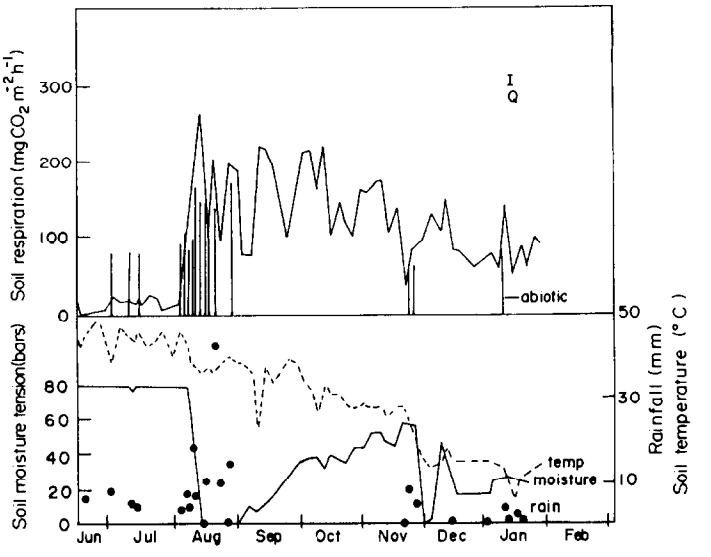

Fig. 2. Rates of carbon mineralization, estimated abiotic carbon fluxes and abiotic factors for a desert soil from June 1981 to January 1982.

(1 bar = 100 kPa)

rarely freeze. Hottest soil temperatures 40°C at 5 cm depth begin June 1 and continue until the summer rains begin (mid-to-late July). Higher soil respiration during the winter than hot dry summer months is the opposite response for most ecosystems (Coleman, 1973; Wildung *et al.*, 1975; Kowalenko *et al.*, 1978; Gupta and Singh, 1981). The half-life and turnover values in this study are uncorrected for root respiration. Root respiration can range from negligible (Feher, 1933) to 50 or 66% of the total soil respiration (Macfadyen, 1970; Turpin, 1920). The latter two studies do not account for the rhizosphere effect on soil microorganisms which may be a larger portion (45–63%) of the CO_2 evolved (Barker and Broyer, 1942; Coleman, 1973).

The use of respiration data to establish carbon turnover overestimates the turnover when compared to litter input data (Witkamp, 1966). However, when root input into the system is accounted for then respiration output is similar to the carbon input of litter and roots (Kirita, 1971). The 5 yr mean annual input of carbon into the soil from roots and litter of creosotebush in the Chihuahuan desert was estimated as 94 g C m^{-2} with a range from 40 to 200 g C m^{-2} (Ludwig and Flavill, 1979). The estimated annual mineralization of C is 300 g C m^{-2} yr which is well above the range of carbon input data. Assuming a steady state, the difference between carbon input and output is an estimate of root and rhizosphere respiration (68% of total) and root respiration would account for 37% of the total if we assume 45% of the rhizosphere respiration is from rhizosphere microflora. We, therefore, corrected the soil respiration data to remove root respiration and recalculated the rate constant: 2.480×10^{-4} day^{-1} which represents a half life of 7.7 yr and turnover of 33 yr for soil organic matter in our system. This corrected turnover was a significant increase over the uncorrected value of 20.7 yr. These values must be considered with caution since overall fertility, as determined by total soil nitrogen, of these soils has decreased over the last 100 yr and, therefore, is not in a steady state.

An attempt was made to determine which abiotic factors best described long term soil respiration. When all data, including that above the optimum temperature, was used good correlations with abiotic factors were observed ($r = -0.67$ for moisture at 15 cm and $r = -0.40$ for maximum temperatures at 5 cm). However, when only data below the optimum temperature was employed, poor correlations were

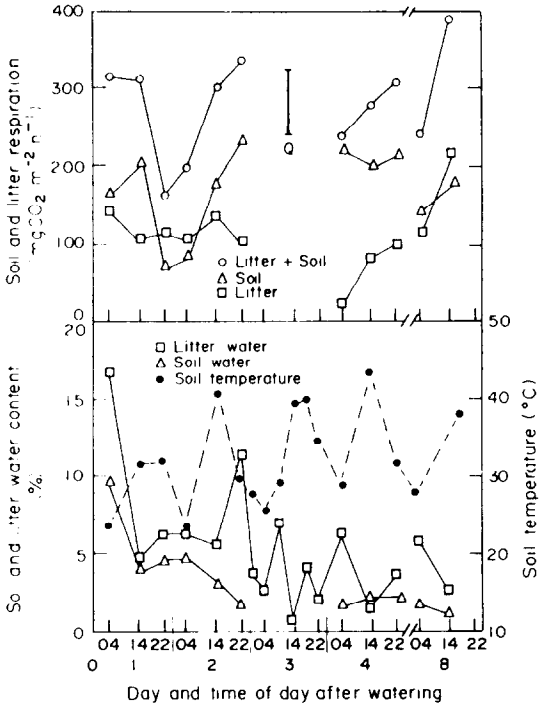

Fig. 3. Diurnal litter and soil respiration and abiotic factors during the dry down after a simulated 2.54 cm rain in July 1979.

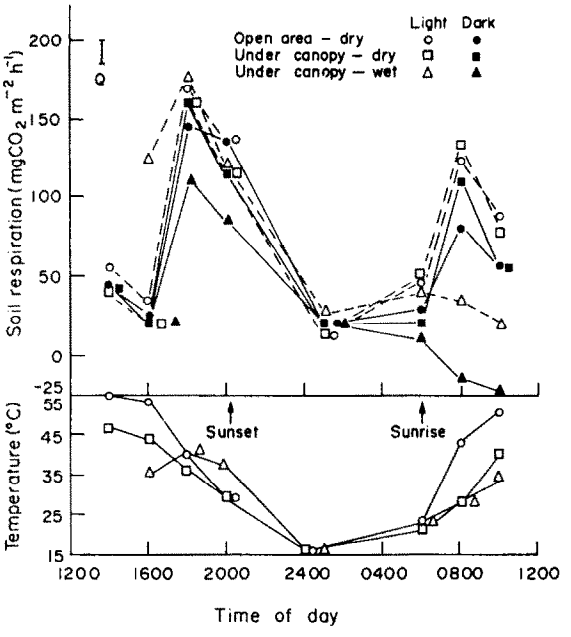

Fig. 4. The effect of location, type of container (light or dark) and simulated rain (2.54 cm) on diurnal soil respiration in July, 1980.

observed ($r = 0.01$ for moisture at 15 cm and $r = 0.07$ for temperature). Soil moisture at 15 cm provided the best regression coefficient for all the data: rate = 52.39 + M15 (−0.492), $r^2 = 0.40$, $P = 0.001$. At temperatures below 40°C moisture at 15 cm provides the best regression coefficient ($r^2 = 0.08$, $P = 0.0002$). Wilding *et al.* (1975) found that temperature and moisture were multiplicative, however, this was not the case in our study. These results indicate that some other factors are important in regulating soil respiration.

To better understand the dynamics of soil respiration and rainfall, we simulated 2.54 cm rain in July, 1979 and measured litter and soil respiration diurnally during the dry down after the rain event. The dynamics of litter–soil respiration on days 1 and 2 were dominated by soil respiration and by litter respiration on days 4 and 8. (Fig. 3). Litter and soil respiration were lowest at 2200 h on day 1 but it was

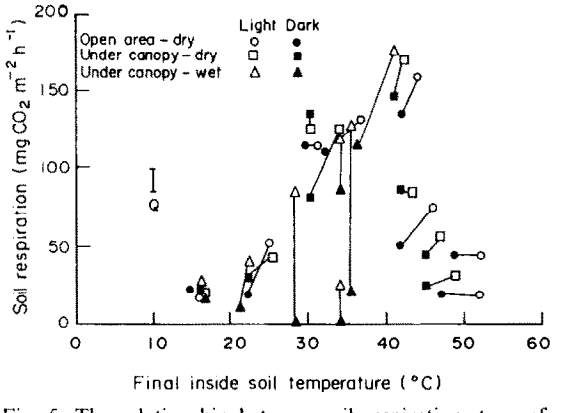

Fig. 5. The relationship between soil respiration, type of container (light or dark), and the soil temperature in the container at the end of the respiration measurements.

highest at this time on days 2 and 4. This was probably in response to dry down on day 1 and may reflect the precipitation of CO_2 as carbonates or perhaps uptake by soil algae. Soil moisture content reached that of unwetted soil by 2200 h on day 2, however, maximum respiration was observed in the soils at this time. After day 1 litter–soil respiration was lowest at 0400 and highest at 2200 h and the soil temperature was highest at 1400 h suggesting that at this time soil temperature may have been above the optimum since diurnal respiration is primarily controlled by temperature (Meyer and Koepf, 1960; Witkamp, 1969). Low soil respiration at 0400 h after day one indicates that the diurnal fluctuations of water in the desert was insufficient to stimulate microbial activity and that diurnal respiration was temperature regulated.

To more fully understand the effects of soil temperature on soil respiration dynamics during dry-down, we wet soils and measured CO_2 output every 2 h for 24 h. Soil moisture increased from 0.42% before watering to 11.35% after watering. Within 24 h the wetted soil moisture had decreased to 3.39%. Two peaks in respiration were observed for the dry treatment, one at 0800 h and the other at 1800 h (Fig. 4). The wetted soils lacked the peak at 0800 h which was 18 h after wetting. The drop in the respiration rate during the afternoon results from soil temperatures being above the optimum. The optimum soil temperature was near 40°C. (Fig. 5). Optimum temperatures for soil respiration near 40 have also been observed for other systems (Koepf, 1953; Elkan and Moore, 1960). There were generally no differences in respiration rates between under canopy and open areas except where temperature related. If soil algal uptake of CO_2 was responsible for the lower respiration rates in the wetted soils then the light container should have less CO_2 than the dark. However, the opposite was observed (Fig. 5). The decrease in CO_2 evolution for the wetted soils, therefore, was not a result of algal fixation but probably chemical precipitation as carbonates. For dry treatments and temperatures below 41°C the difference between the rates for light and dark containers were related to the difference between the final temperature for light and dark containers ($r^2 = 0.71$, $P = 0.0001$); the regression was (Δ rate = 2.29 + 8.84 Δt). This suggests that temperature was the major factor contributing to the difference in rates between light and dark containers. Soil moisture for dry soils was independent of time of day and type of container ($x = 0.42\%$ on an oven dried weight basis). A much greater difference in rates was observed when soils were wet than dry. This difference in wet soils was relatively independent of soil temperature suggesting a stimulation of soil respiration in the presence of light. The light–dark container method used in this study though shown to be useful in aquatic studies appears to be non-applicable to soil systems due to temperature problems.

The only treatment differences for energies of activation (E_A) and A values were between the light wetted and dry soils (Table 1). The higher E_A for the dry soils suggests that a higher energy input is required for the decomposition of soil organic matter in soils. This may be a function of higher mainte-

Table 1. The effect of light and dark containers, simulated rain (2.54 cm) and location on the activation energy (E_A) and the constant A for carbon mineralization in a desert soil

Location	Type of container	Dry E_A kJ mol^{-1}	Dry A mg C m^{-2} h^{-1}	Dry r^2	Wet E_A kJ mol^{-1}	Wet A mg C m^{-2} h^{-1}	Wet r^2
Under canopy							
	Dark	56.66	11.59	(0.64)	68.24	13.33	(0.50)
	Light	84.91	16.58	(0.80)	39.51	8.56	(0.30)
Open area							
	Dark	70.55	13.96	(0.57)	ND	ND	ND
	Light	73.02	14.49	(0.82)	ND	ND	ND
Overall		69.38	13.83	(0.64)	54.63	11.08	(0.38)

nance energy requirements (such as water conservation) in the drier soils. Parker and Doxtader (1983) have also observed an increase in E_A and A values with decreasing soil moisture content for 2,4-D degradation under laboratory conditions. There was no difference between under bush and open areas for E_A and A values (Table 1) with the mean E_A and values of 69.38 kJ mol^{-1} and 13.83 mg m^{-2} h^{-1} respectively. Unfortunately due to a lack of activation energy values for field studies in other ecosystems, comparisons with these systems cannot be made. The use of results of diurnal studies appears to be more beneficial in investigating temperature, moisture and respiration relationships than long term studies.

One problem with measuring CO_2 output as an indicator of respiration in desert soils is their high carbonate contents. The soil used in this study contained 2.3% carbonates. For long term studies abiotic CO_2 fluxes following rain should be counteracted by net CO_2 uptake by soil the day after a rain to re-establish equilibrium. Over the long run net abiotic inputs and outputs should be equal and therefore not affect the use of CO_2 data in estimating soil organic matter turnover. However, abiotic CO_2 dynamics can dramatically affect the interpretation of diurnal respiration studies. Since diurnal respiration is temperature regulated, we determined the relationship between temperature and abiotic carbon fluxes in sterilized soil. There appeared to be a threshold temperature (between 22 and 45°C) above which abiotic fluxes of CO_2 increased drastically (Fig. 6). The relationship between soil temperature (T) 22°C and abiotic fluxes of CO_2 on day 1 was best described by:

$$\text{mg } CO_2\ m^{-2}\ h^{-1} = \exp(3.61 + 0.0428 \times T) \quad (4)$$

Estimated abiotic carbon dynamics are shown in Fig. 2. On three dates in July we estimated higher abiotic carbon than observed CO_2. The rains on these dates did not infiltrate as deep as the same intensity rains did on other dates as indicated by soil moisture tension. Evaporation was probably very high on these dates due to elevated soil temperatures.

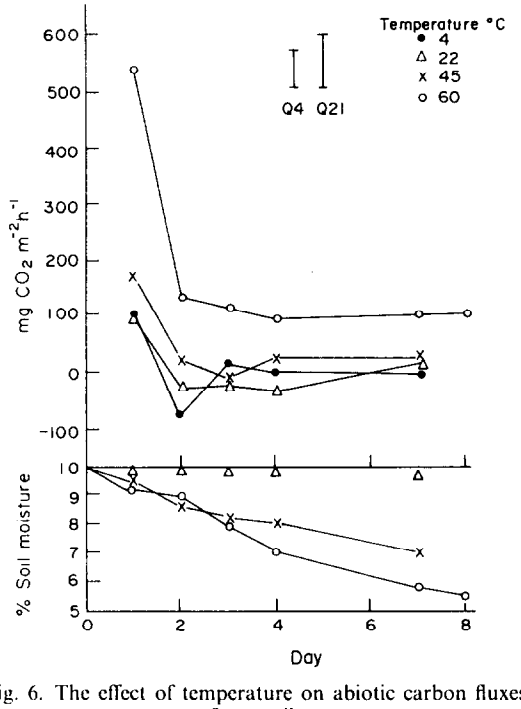

Fig. 6. The effect of temperature on abiotic carbon fluxes from soil.

We conclude that the turnover of soil organic matter in warm desert rangeland was 20 yr as estimated by soil respiration data and 33 yr after correcting for root respiration. Diurnal soil respiration was controlled by soil temperature with two peaks in activity: one just before and the other immediately following above optimum afternoon temperatures. The optimum temperature was near 40°C. The activation energy was 84.91 kJ mol^{-1} for dry soil which decreased to 39.51 kJ mol^{-1} when the soil was wetted. Diurnal soil respiration was independent of the diurnal fluctuations of soil water. Respiration in wetted soil decreased at the end of the first day after wetting. This decrease could not be explained by soil temperature or algal fixation of CO_2. However, the use of the light–dark container method, as used in this study was found to be non-applicable to measuring soil algal uptake of CO_2.

Acknowledgement—This research was supported by a grant from the U.S. National Science Foundation Ecosystems Program to W. G. Whitford.

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