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Comparison of Microbial Activity in Desert Soils of the Western United States

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COMPARISON OF MICROBIAL ACTIVITY IN DESERT SOILS OF THE WESTERN UNITED STATES

by

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ABSTRACT

Comparison of Microbial Activity in Desert Soils

of the Western United States

by

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Soils from four regional deserts, Great Basin, Sonoran, Chihuahuan, and Mojave, were collected at times throughout the year which would best exhibit microbial response to moisture or vegetation. The soils were analyzed for several chemical and physical properties. Biological and biochemical characteristics, namely respiration, dehydrogenase activity, adenosine triphosphate concentration, proteolytic activity, nitrification potential, and microbial numbers, were measured.

The soils exhibited fluctuations in microbial activity as measured by respiration, dehydrogenase activity, adenosine triphosphate concentration, proteolytic activity, and nitrification potential during different moisture seasons.

Increase in soil moisture as modified by precipitation did not cause a significant difference in respiration or proteolysis between desert soils, however, an increase in moisture did cause a significant difference in nitrification potential of desert soils. Proteolytic activity was highest in soils collected when above-ground portions of desert plants were dormant.

Low nitrification potential of desert soils was found. Nitrite accumulation in perfusion experiments but not in the field was observed.

Respiration, dehydrogenase activity and adenosine triphosphate concentration did not respond proportionally in desert soils adjusted to different moisture levels. These results suggest that respiration, dehydrogenase activity and ATP concentration each appear to represent a different phase of microbial metabolism in desert soils.

(130 pages)

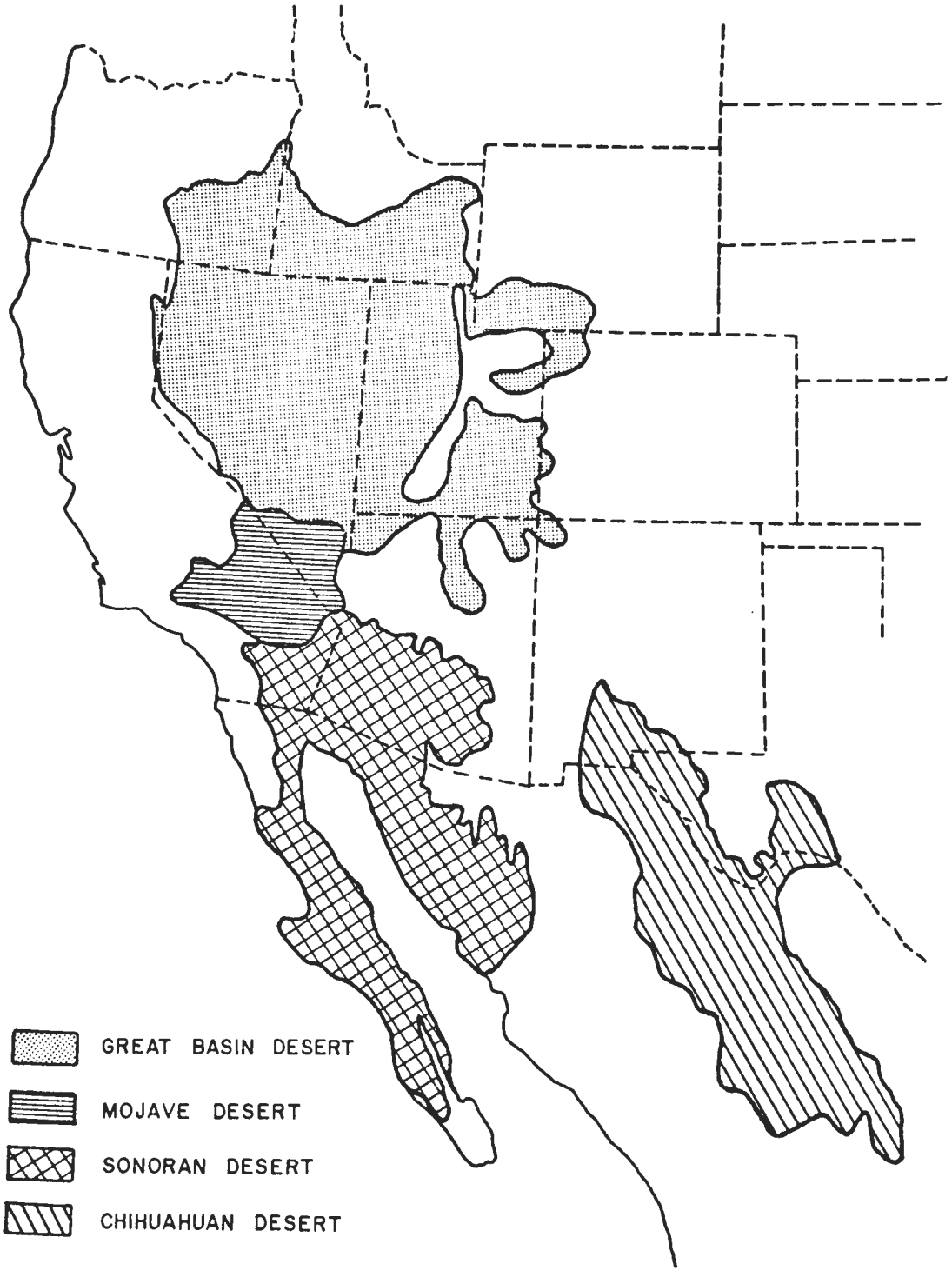
INTRODUCTION

Although microbial activity in desert soils is often taken for granted, it is an integral part of decomposition and nutrient transformation processes. Information pertaining to microbial activity of the soil is scanty, in spite of several recent reviews on desert ecosystems (Costello 1972, Dregne 1970, McGinnies et al. 1968, Brown 1974, Noy-Meir 1973, Noy-Meir 1974, Noy-Meir 1978, Fuller 1975).

In response to increasing population and advancing technology there is an accelerated interest in the desert as a potentially productive land form. Balogh (1970) speculates that significant desert areas will come under irrigation and thus play an important role in food production. It is therefore important to learn more about the microbial aspect of desert soils to aid in avoiding possible irreparable ecological damage.

There are four distinct desert types or regional deserts found in the western United States (Shreve 1942, McGinnies et al. 1968). The southernmost deserts are the Sonoran and Chihuahuan. The northernmost desert is the Great Basin. The fourth desert, the Mojave, is sometimes considered as a transition between the Great Basin and Sonoran Deserts (see Figure 1). Vegetation suggests transitional character of the Mojave. *Artemisia tridentata*, one of the dominants of the Great Basin, mingles with *Larrea divaricata*, characteristic of southern deserts. On the other hand, the Chihuahuan desert may have been a part of a

Figure 1. Deserts of the western United States and northern Mexico (Adapted from Shreve 1942, cited by Hastings and Turner 1965).


GREAT BASIN DESERT
MOJAVE DESERT
SONORAN DESERT
CHIHUAHUAN DESERT

larger complex extending from the northernmost edge of the Mojave through the Sonoran since all these divisions are tied together by *Larrea divaricata* existing as several races adapted to widely varying conditions of temperature and moisture (McLeary 1968; Hastings and Turner 1972).

Climate, topography, and dominant vegetation differ in each of these deserts. For example, the average elevation of the Great Basin desert is above 1200 m, that of the Sonoran below 600 to 900 m, and that of the Chihuahuan 900 to 1200 m above sea level. In addition, temperatures in the Sonoran desert are generally higher than any other desert region of the United States. Rainfall in the interior portions of the Sonoran Desert are about equally divided between winter months (December-March) and summer months (July-September). Temperatures in the Chihuahuan are lower than in the Sonoran, but most of the precipitation is confined to late summer-early fall months. Both the Great Basin and the Mojave deserts are characterized by hot summers and comparatively colder winters than the deserts to the south. Precipitation occurs primarily in the winter there (McLeary 1968).

Dominant plants that characterize each of these deserts are: Chihuahuan--*Larrea divaricata, Flourensia cernua, Acacia* spp. and *Mortonia scabrella;* Sonoran--*Larrea divaricata, Ambrosia deltiodea, Cereus* spp., and *Opuntia* spp.; Mojave--*Larrea divaricata, Lycium andersonii,* and *Krameria parvifolia;* Great Basin--*Artemisia tridentata, Atriplex confertifolia,* and *Ceratoides lanata* (McGinnies 1968).

Since little was known about soil microorganisms in these deserts, this study was undertaken to investigate certain aspects of microbial

activity in several desert soils of the western United States. These aspects include decomposition and nitrogen transformation, especially nitrification.

The first objective of this study was to assess the effect of moisture season on microbial activity measured by respiration, dehydrogenase activity, ATP concentration, proteolytic activity, nitrification potential, microbial numbers, and organic carbon and nitrogen content in desert soils, and to see what similarities existed between desert soils in the regional deserts, as characterized by these parameters. It was hypothesized that microbial activity as measured by dehydrogenase activity, respiration, and ATP concentration in desert soils of different desert regions collected during the wet seasons would not be significantly different. Furthermore, it was hypothesized that proteolytic activity and nitrification potential in desert soils of different desert regions would be significantly different during the wet seasons. It was hypothesized that parameters measuring decomposition, such as respiration and proteolysis, would be highest in soils collected during the seasons in which above-ground portions of higher plants were dormant.

The second objective was to study effects of moisture on microbial activity of desert soils under laboratory-simulated field conditons. Soil microbial activity under these conditions was measured by three parameters: respiration, dehydrogenase activity, and ATP concentration. The laboratory experiments enabled simulation of wetting-drying cycles in the desert. It was also possible to adjust the moisture levels in

the soils and observe microbial response. It was hypothesized that respiration, dehydrogenase activity, and ATP concentration would increase significantly in desert soils moistened to less than -2 bars. In addition, it was hypothesized that microbial activity, as measured by respiration, dehydrogenase activity, and ATP concentration, would decrease initially upon desiccation of soil, but upon further desiccation would not significantly decrease further.

Soil samples were collected over one year during both the vegetatively active and vegetatively dormant seasons in the Chihuahuan, Sonoran, Mojave, and Great Basin deserts. The soils were brought to the laboratory and analyzed. Soils from two of the sampling dates were used to conduct additional experiments.

Since only a one-year cycle of microbial activity was measured, the data does not indicate annual trends. It was impossible to sample soils within a period of one year at all moisture seasons at each desert site in all moisture conditions.

LITERATURE REVIEW

Soil microorganisms play a major role in the transfer of energy and transformation of nutrients in terrestrial ecosystems. In order to quantitatively characterize the microbial contribution to these processes, information is needed on the abundance and activity of the soil microbiota.

Smith (1968) states that detailed characteristics of the desert environment are a function of the interaction of the bedrock geology and surface processes through time. Differences between different deserts and between different parts within the same desert represent divergent patterns of this interaction. Desert soil profiles are characterized by the limited extent to which parent materials have been altered by soil-forming processes.

In conditons of extreme moisture deficiency and heat, the production of the organic mass declines accordingly and the biological cycle becomes constricted (Rodin and Basilevich 1965). Miller and Johnson (1964) point out, however, that maximum biological activity can be expected to take place at the lowest moisture tension where aeration is sufficient.

Charley (1972) states that community nutrition is determined by chemical status and biological activity of the surface soil. According to Reichle (1975) depletion of the carbon pool decreases the productivity and stability of the ecosystem. Consequently, decomposition and mineralization processes control the nature of the nitrogen cycle.

Dregne (1970) states that the desert is naturally rich in most essential nutrient elements except nitrogen.

The principal factor limiting bacterial growth in soil is scarcity of food or the lack of a suitable and available source of energy (Clark 1967), but overall functioning of arid ecosystems is limited more by the availability of water and mineral nutrients (West 1978).

Cameron (1961) claims organisms can have little or no influence on the soil-forming process in extremely arid deserts, therefore little profile development may be observed. In most arid soils, a large proportion of nutrients in both organic and mineral forms is concentrated in the surface layer (0-5 cm) (Skujins 1972, Charley and Cowling 1968).

The relationship of desert shrubs to soil characteristics has been studied by several authors. Tiedmann and Klemmedson (1973) found striking differences in soils under mesquite and open areas, with more available nutrients under mesquite. Garcia-Moya and McKell (1970) state that the difference in nitrogen content under different shrubs appears to be dependent on the root system. In addition, Roberts (1950) indicated that shrubs such as greasewood and shadscale are directly responsible for significant changes in some of the chemical characteristics of the soil profile.

Charley and West (1975) found significant concentration of nitrogent under individual shrubs in the desert shrub communities studied. The contents of nitrogen, carbon and available organic phosphorus, and total phosphorus concentrated towards the top few centimeters of the soil profile. Rixon (1971) also found oxygen uptake and nitrification

if they required a pF of less than 4.2. He also noted that ammonifying organisms are prevalent and active in arid-zone soils whereas nitrite- and nitrate-producing organisms are frequently inactive.

Clark and Kemper (1967) state that different microorganisms respond differently under conditions of dry soil and all microbial transformations are not stopped during drying out of soil. Ammonification can proceed under drier conditions than nitrification. Pauli (1964) suggested that the intensity of microbial action is dependent greatly on the hydrothermic conditions which prevail in the surface 0-15 cm. Microorganisms show full activity when soil pF is about 3.0. He also found that temperatures of 30^{o}C are optimum for stimulation of activity.

Dommergues (1960, 1962) has demonstrated that certain microbial groups can function at soil moisture contents considerably lower than wilting point in soils of arid and semiarid parts of West Africa. McLaren and Skujins (1968) and Ekpete and Cornfield (1965) state that microbial activity increases with water content to about 60 to 80 percent water holding capacity. Lowered biological activity at low water contents is principally a question of moisture stress. It is apparent that the longer a soil remains dry, the greater the decomposition activity following "wetting-up" (Charley 1972).

Dommergues (1969) states that stimulation of organic matter mineralization is very intense in semiarid and arid soils when desiccated soils are "rehumidified" either by rain or by irrigation, especially in a year where there are numerous cycles of wetting and drying. Birch (1958) suggests that low rainfall is usually associated with

in soils underneath *Atriplex vescaria* were greater than those from the interspace. This was true only for the surface 7.5 cm. Charley and West (1977) showed similar differences for other desert shrubs in Utah. Nishita and Haug (1973) studied desert soils at the Nevada Test Site and found total nitrogen in soil under *Krameria parvifolia* to be greater than that under *Larrea divaricata*, indicating differences due to plant species.

Edaphic factors which are prominent in arid zones operate almost always by modification of the water regime (Noy-Meir 1973). In a grassland site on the Arid Land Ecology Reserve in south central Washington, Wilding et al. (1973) found soil water to be a limiting factor in the late spring, summer, and early fall when soil temperatures were above 15°C. Similarly, Thayer (1974) found effects of extreme drought to be controlling factors in a grassland ecosystem since decomposition, respiration, and microbial biomass changes were all apparent responses to rainfall and available moisture. Franz (1971) made investigations of seasonal variation of microbial life in several natural and cultivated soils in three different climatic zones of Chile and found moisture to be a controlling factor. Birch and Friend (1956) studied East African soils and found rainfall to be the major influence on soil organic matter.

Seasonal dynamics of enzymatic activity of soils in different climatic zones of Armenia have been determined (Galstian 1974). Soil enzymes were found to be the most active at the end of sping and beginning of summer and in the second half of summer activity decreases slightly but in autumn it increases again. O'Brien (1973) studied

proteolytic activity in a desert grassland site and found activity to increase after summer rains and remain at higher levels throughout the summer.

Utter (1972) studied microbial activity in Curlew desert soil and found peak months for microbial populations to be January through April, whereas low counts occurred in July, August, and September. Soils collected in October and November had the highest concentration of ATP.

Nitrification and ammonification rates in arid Southern Curlew Valley Utah soils were studied by Patel (1972). She found nitrification rates higher during the spring and early summer period than in the fall.

Water is usually the most limiting factor for all life in desert environments. However, microorganisms seem to be able to survive the xeric conditions they encounter. For example, in studying the microflora of an Egyptian arid soil, Naguib and Mouchacca (1971) showed the presence of an active fungal flora in the desert soil and the density of the fungal population in the samples was related to its local microenvironment, edaphic, and climatic conditions as well as plant cover. Vela (1974) reported that viable *Azobacter* were detected in soils stored in the laboratory for more than ten years and suggested that these bacteria could exist in a dormant nature for prolonged periods of time.

Dregne (1968) classified microbial groups in Mauritania soils as hyperxerophilic if they grew at a soil moisture pF greater than 4.9, xerophilic if they grew at a pF between 4.2 and 4.9, and hygrophilic

greater frequency of wet and dry periods than high rainfall and that it should therefore be conducive to an accelerated carbon loss.

Sorensen (1974) found that repeated air drying and rewetting of three soils followed by incubation at 20°C resulted in an increase in the rate of decomposition of a fraction of ^{14}C-labelled organic matter in soils. Birch (1958, 1959a, 1959b) also found increased decomposition of organic matter following successive drying and wetting and concluded that the longer soils are dried, the greater is the subsequent decomposition and nitrogen mineralization when they are remoistened. In a later publication, Birch (1960) suggests that the magnitude of decomposition on moistening a dry soil is largely a function of carbon content of the soil. In addition, he found that the rate of nitrogen mineralization after moistening falls off more rapidly than that of carbon mineralization.

There have been several explanations for the phenomenon of increased activity in dry soil upon rewetting. Soulides and Allison (1961) indicate that decomposition of soil organic matter following intermittent drying is due primarily to the release of nutrients, especially energy sources, that can be rapidly oxidized by microorganisms. Similarly Birch (1958) suggests that successive dryings effected the release of small amounts of decomposable material from within the clay lattice where it was protected from microbial attack. But, he states, the flush of decomposition following the wetting of a dry soil is not due to the effect of drying on the physical or chemical properties of the organic substrate, otherwise a cumulative effect would be expected. According to Stevenson (1956) air drying brings: a) small changes

the solubility of mineral substances; b) large increases in solubility of organic substrates; c) large increases in nitrogen and phosphorus; d) large increases in NH_4-N and amide N; and 3) sharp decreases in microbial numbers. McLaren and Skujins (1968) point out that increased microbial activity upon rewetting may be due to disruption of aggregates during drying and thereby making the organic substrates accessible to microorganisms when rewetted. Hayashi and Harada (1969) state that the magnitude of flush of decomposition depends on the water potential at which the soil is dried. The lower the water potential, the greater the flush.

The microbial population in desert soils may vary more widely than in any other climatic zone (Fuller 1974). Low numbers are associated with extremely low and irregular rainfall and paucity of higher plant life.

The microbial population of desert soils has been ranked in decreasing order of abundance: aerobes plus actinomycetes, anaerobes, faculative anaerobes, algae and fungi (Cameron and Blank 1965).

Pochon, de Barjas, and Lajudis (1957) found no *Azotobacter*, *Clostridia*, or nitrifying organisms under extreme arid Saharan conditions in the surface 10 cm of soils and the activity of ammonifying, denitrifying, cellulolytic, and amylolytic organisms was very low. High numbers of rhizosopore organisms were found as compared to low numbers in adjacent soil (Vargues 1953). Similar results were obtained by Elwan and Mahmoud (1950) in an Egyptian desert study in which *Azotobacter* and *Clostridium* species were isolated from the rhizosphere, but not from the surrounding soil. In the arid zones of

Morocco, aerobic cellulolytic bacteria were present but no *Azotobacter* (Sasson 1960).

For many ecological studies it is necessary to know the biomass and rate of metabolic activity of various types of organisms. Adenosine triphosphate is a ubiquitous component of living cells and is not present in dead cells. ATP has been suggested as a reasonably reliable microbial biomass indicator in soils, lake sediments, and aquatic environments (Holm-Hansen 1969, Lee et al. 1971a, 1971b, and Jassby 1975). The quantitative analysis for ATP in submicrogram quantities depends upon the measurement of the light emitted when ATP is added to an enzyme preparation containing luciferase and luciferin obtained from ground-up firefly *(Photinus pyralis)* lanterns. The ATP-firefly bioluminescence procedure as first described by Seliger and McElroy (1960) is outlined in the following reactions,

$$E + ATP + LH_2 \xleftrightharpoons{Mg^{++}} E\text{-}LH_2\text{-}AMP + PP$$

$$E\text{-}LH_2\text{-}AMP + O_2 \xleftrightharpoons[pH]{neutral} E\text{-}L\text{-}AMP + H_2O + h\nu$$

where

E = enzyme luciferase

LH_2 = luciferin (reduced)

PP = pyrophosphate

L = dehydroluciferin

ATP analysis gives the total biomass only and gives no information about the number of kinds of cells present.

Lee et al. (1971b) state that ATP data should also be useful as an index of total biomass for evaluating the effect of any environmental, nutritional, or toxic variable on the total microbial life flux in the system. Brezonic, Brown and Fox (1975) suggest that ATP activity is a relative indicator of nutrient deficiency due to rapid response of ATP in nutrient deficient cultures after additions of nutrients. ATP measurements combined with a knowledge of the total amount of nutrient present in the system should enable estimation of the relative amounts of nutrients present in the living compared with the nonliving phase of the system (Lee et al. 1971b).

Doxtader (1969) and Sparrow and Doxtader (1973) found a direct relationship between bacterial numbers estimated from dilution plates and ATP concentration in grassland soils. Contrarily, Utter (1972) found poor correlation between ATP and CO_2 evolution and between ATP and in microbial numbers in his work with Curlew desert soils. Conklin and MacGregor (1972) examined several extraction methods for ATP in desert soil. They concluded that soil moisture level and texture appear to have little effect on recoverability of ATP from the desert soils examined.

In a few desert environments direct oxidation of soil organic matter occurs to a small extent and some decomposition is carried out by extracellular enzymes from microorganisms (MacFayden 1971). A recent review of soil enzymes exists (Skujins 1976).

Measurements of carbon dioxide evolution or oxygen uptake are techniques employed to measure soil respiration. Organic matter degradation is a property of all heterotrophs and respiration is commonly used to indicate the level of microbial activity. Respiration is a useful tool in studying the intensity of metabolism (Anderson and Domsch 1973, 1974, 1975). Stotzky (1965) indicates that respiratory rates reflect the microbial activity rather than numbers, types, or growth of soil microbiota.

Evolution of carbon dioxide is largely dependent on the biological life of the soil (activity of microorganisms, soil fauna, root respiration, etc.); however, most investigators believe that activity of microorganisms is the main source of CO_2 release (Artyushenko 1969). According to Lundegardh (1927), two-thirds of carbon dioxide present in soil air is formed as a results of microbial activity while one-third is released by plant roots. Similarly, Coleman (1973) reported that root respiration never exceeds 17 percent of the total in oak forest and old field soil cores. It has been difficult to measure exactly what contribution each type of organism makes to the total respiration of the soil, even though attempts have been made.

One difficulty with using respiration to estimate biological activity is that respiration is an aerobic process and anaerobic conditions may exist frequently in soil crumbs because there is an uneven distribution of water and consequently a presence of anaerobic zones (Greenwood 1968).

Dehydrogenase activity is another parameter thought to reflect the total biological activity of the soil (Skujins 1967). Stevenson

(1959) reported evidence for the reliability of the dehydrogenase test as a means of estimating total microbial activity in soils. He was able to show significant correlation between O_2 uptake and dehydrogenase activity. In addition, he also showed significant correlation between dehydrogenase and oxygen uptake in soils treated with fresh crop residues indicating that as microbial activity fluctuates due to decomposition of the organic material corresponding changes occur in dehydrogenase activity and oxygen uptake. Dehydrogenase enzymes play an essential role in the initial stages of the oxidation of soil organic matter by transferring hydrogen or electrons from substrates to acceptors (Ross 1971).

Dehydrogenation in the soil is associated with the active vital functions of its microorganisms. Peterson (1967) suggested that dehydrogenase activity of the soil should be interpreted as dehydrogenase activity of the microflora in the soil sample since the dehydrogenases are not present in the soil prior to the beginning of the experiment. Moreover, experiments made by Peterson (1967) showed that nonsterile roots of all the plants used exhibited dehydrogenase activity wherease sterile roots of all plants tested except for clover did not. Thus, the dehydrogenase activity on the nonsterile roots was probably attributed to the rhizosphere organisms and not to the roots.

Unfortunately, attempts to correlate dehydrogenase activity with other biological parameters in cultivated and well-irrigated soils generally have not been successful (Skujins 1967). Furthermore, Moore and Factors (1972) concluded that dehydrogenase activity was not useful as a general index of soil fertility. In arid soils, however, where activities are associated with certain horizons and change by order of

magnitudes in their vertical distribution, Skujins (1973) reports that dehydrogenase activity appears to be a useful criterion for the characterization of soil biological status and for the prediction of several biological activities such as proteolytic, nitrifying, and respiratory activities.

The termination of the reactions involved in organic nitrogen mineralization occurs at the point where ammonium is formed (Alexander 1961). Ammonium then serves as a starting point for a process known as nitrification, the biological oxidation of ammonium to nitrate. The process of nitrification has been extensively studied and reviewed by various investigators, for example, Aleem (1970), Broadbent et al. (1957), Dommergues (1960), Justice and Smith (1962), Lees and Quastel (1946) and Quastel and Scholefield (1951). The studies of these processes have dealt mostly with agricultural, forest, and grassland soils. Very few have dealt with desert soils (Patel 1972, Skujins and Trujillo y Fulgham, 1977).

Nitrification rates vary among the different climates and types of soils examined. It is evident, therefore, that the environmental factors which are characteristic of different climatic regions and/or soil types determine the rate or degree at which nitrification does occur. Such environmental factors include pH, oxygen supply, soil moisture regime, temperature, organic matter level or supply, CO_2 content, and the cation exchange capacity of the soil (Mahendrappa, Smith and Christiansen 1966, Skujins and Trujillo y Fulgham 1977). These factors may affect the nitrification by acting upon the initial bacterial population and/or their subsequent proliferation.

For example, Morrill and Dawson (1962) found that the rate of nitrification is closely or directly correlated with the pH of the soil and the optimum pH for most of the ammonium oxidizing organisms lies above neutrality while that for the nitrite oxidizers is close the neutral. Martin, Buehrer, and Caster (1942) report the existence of threshold pH value of 7.7 $\pm$ 0.1 for nitrification of ammonia in alkaline desert soils.

Mahendrappa et al. (1966) showed that soils from the northern section of the western United States nitrified more rapidly at cooler temperatures (20^{o} to 25^{o}C) than at higher temperatures (35^{o} to 40^{o}C) whereas the Southern region soils nitrify faster at temperatures above 35^{o}C. In addition, Mahendrappa (1963) found that when nitrifiers are transferred to another soil, they will function in the way they did in the original soil. That is, if they nitrified more rapidly at 25^{o}C than at 35^{o}C they will continue to show this temperature response. Dommergues (1969) states that arid and semiarid strains of soil microorganisms are thermotolerant.

Maximum nitrate production was found to occur at moisture tensions of -0.5 to -0.15 bar (Dubey 1968, Miller and Johnson 1965, Sabey 1969). However, activity of nitrifying microorganisms continues at moisture levels much lower than wilting point, the lower limit for growth of higher plants (Dubey 1968), and even at moisture levels below that (Domergues 1960).

Sims and Collins (1960) indicated that drought, high temperature, and other extensive variations in environmental conditions had a relatively minor effect on the numbers and distribution of nitrifying organisms.

MATERIALS AND METHODS

Decomposition and mineralization in soils are microbial processes that are modified by the water regime. Seasonal fluctuations of moisture also modify the vegetation which in turn influences microbial processes. Soils from five desert sites were sampled at certain times throughout the year which would best exhibit microbial response to moisture or vegetation.

Descriptions of Study Areas

The four study sites used were established IBP Desert Biome Validation Study sites at Las Cruces, New Mexico - Jornada; Tucson, Arizona - Silvebell; Mercury, Nevada - Rock Valley; and Milford, Utah - Pine Valley (Desert Experimental Range). Another site was used in Curlew Valley, Utah, and is a research area maintained by the Department of Range Science, Utah State University, Logan. Sampling stations were randomly selected where the most dominant species were represented. Samples were collected from the interspaces between shrubs at a 0-5 cm depth.

1) Jornada - The Jornada Validation area, representative of the Chihuahuan Desert, is located on the New Mexico State University Jornada Experimental Ranch. There are two designated sites within the area: playa and bajada.

The playa site is characterized by being approximately 300 m lower than the bajada. The playa is a depression where standing water may

accumulate to a depth of 30-45 cm during the rainy season. This periodic inundation has produced a dense vegetal cover and a well-developed soil.

Dominant species of vegetation of the playa bottom, where a 12 m^2 sampling station was located, include *Panicum obtusum*, *Xanthium strumarium*, and *Hymenoxys oderata*. *Panicum obtusum* contributes most to the standing crop, but there are other perennials such as *Sida leprosa*, *Cyperus exculentus*, *Hoffmanseggia densiflora*, and *Hilaria mutica* which may dominate the playa bottom, depending on soil moisture recharge (Whitford et al. 1973).

Playa soils initiated development in mid-Pleistocene (Hawley and Gile 1966, Gile et al. 1970, and Ruhe 1967, all cited by Whitford et al. 1973). These soils have strong genetic horizons with the carbonate accumulation horizons being most distinctive. In some areas, the argillic horizon has been partly or completely engulfed or has been mixed by soil fauna, or both (Whitford et al. 1973).

The bajada site is described as an alluvial fan dissected by large arroyos (washes) and smaller arroyos which converge on the large arroyos. Areas between the arroyos are the upland areas. Station 1 is less than 100 m from a small arroyo on an upland area. Station 2 is on the edge of a large arroyo, and Station 3 is an upland area 200-300 m from any arroyos.

Principal plant species at Station 1 include *Larrea divaricata*, *Flourensia cernua*, *Yucca elata* and *Yucca baccata*. Station 2 dominants include *Chilopsis linearis*, *Fallugia paradoxa*, and *Prosopis glandulosa* var. *torreyana*; and the dominant shrub at Station 3 is *Larrea divaricata*.

Bajada soils are dated from mid- to late-Pleistocene (Hawley and Gile 1966, Gile et al. 1970, and Ruhe 1967, all cited by Whitford et al. 1973). They have prominent horizons of silicate clay accumulations and prominent carbonate accumulation horizons commonly within about 61 cm of the surface. The surface texture is typified as sandy loam. Station 1 soils are shallow, with a caliche layer 5-100 cm in the profile. Generally, along the arroyos, which is characterized by Station 2, there is no caliche layer. Station 3 soils are deep soils with a caliche layer beginning at 3 m (Whitford et al. 1973).

The prevailing pattern of precipitation of the Jornada area is for the highest amount of precipitation to uccur during the months of July through October and the lowest rainfall to occur in April through early June. The long term average annual precipitation in the vicinity amounts to 200-250 mm.

2) Silverbell - The Silverbell Validation Site, representative of the Sonoran Desert, is located near the Silverbell Mountains northwest of Tucson, Arizona. A 12 m^2 sampling station was established in the southeast corner of the Silverbell Validation Site.

Principal plant species of the area include *Franseria deltoidea, Larrea divaricata, Cercidium microphyllum, Acacia constricta, Olneya tesota, Cereus gigantea,* and numerous species of *Opuntia.*

The soils in the sampling station location are described to have been formed in calcareous alluvium. The primary rocks in the alluvium are andesite, basalt, granite, and quartzite. The soil profiles at this site are calcareous throughout. The maximum carbonate accumulation generally occurs at a depth of 30-50 cm. In some areas, the

carbonates form a weakly cemented layer at that depth. The soils are well drained and have moderate permeability. Yearly precipitation in the vicinity averages 200-400 mm, with largest amounts occurring during July, August, and December (Thames et al. 1973). This pattern of moisture results in a lesser spring peak of activity in the Sonoran Desert.

3) Rock Valley - The Rock Valley Validation Site, representative of the Mojave Desert, is located at the southern portion of the ERDA Nevada Test Site in Nye County, Nevada.

The dominant shrubs of the area where a 12 m^2 sampling station was located include *Larrea divaricata, Ambrosia dumosa, Krameria parvifolia, Lycium andersonii, Lycium pallidum* and *Ephedra nevadensis* with *Bromus rubens* and *Vulpea octaflora* being the dominant grass species (Turner et al. 1973).

Soils of this site are derived from a heterogeneous, highly calcareous alluvium composed primarily of Cambrian limestones with some tuff and basalt. The soil's surface is a well-developed desert pavement underlain with a massive and strongly cemented petrocalcic horizon at depths ranging from 30-70 cm. The caliche is virtually impervious to plant roots, but serves as a restrictive layer preventing moisture loss to greater depths in the soil. These soils also have considerable amounts of amorphous clays with a low cation exchange capacity (Turner et al. 1973).

The general precipitation pattern at the Nevada Test Site has the greatest amounts occurring from August through November and least

occurring from April through early July. The annual average precipitation ranges from 200-250 mm per year (Turner et al. 1973).

4) Pine Valley - Pine Valley Validation Site, representative of the southern Great Basin Desert, is located in the Desert Experimental Range in Millard County, Utah.

Dominant shrubs of the area (where a 12 m^2 sampling station was located) include *Atriplex confertifolia, Ceratoides lanata, Artemisia spinescence,* and *Sphaeralcea grossulariafolia.* The dominant perennial grass is *Hilaria jamesii* (Frischknecht 1975).

Baseline data characterizing the soils of this validation site were not available at the time of this writing, although a soil survey does exist for the Desert Experimental Range (USDA Soil Conserv. Serv. and Forest Service).

The greatest amounts of precipitation in Pine Valley usually occur during July through October with the least amount occurring in May. Average precipitation is 154 mm per year (Holmgren and Brewster 1972).

5) Curlew Valley - The area where soil samples were collected is about 36 km south of the Utah-Idaho border and 32 km southwest of Snowville, Utah. Curlew Valley, representative of the northern Great Basin Desert, is a broad, flat lacustrine valley extending northward into Idaho from the salt flats on the north edge of the Great Salt Lake. Zonation is typical of many valleys of the Great Basin Region.

Three plant community types are located contiguous to each other within the research area. Samples were taken from within three exclosures with vegetation dominated by nearly pure stands of big sagebrush

(Artemisia tridentata), shadscale *(Atriplex confertifolia)*, and winterfat *(Ceratoides lanata)*, respectively. Detailed soil descriptions are given by Mitchell et al. (1966) and Charley and West (1975).

Annual precipitation in Southern Curlew Valley averages around 300-350 mm, occurring mostly during the winter in the form of snow (Balph 1973).

Sampling station designations are given in Table 1 and collection periods are given in Table 2. Total monthly precipitation records were obtained from weather stations at or near each site in order to compare yearly precipitation patterns during the collection period with the long-term averages. For statistical comparison, seasons were assigned to each collection date based on the precipitation data for the year and on the growth or dormancy of above-ground portions of major vascular plants at that time of collection.

Table 1. Sampling station designations

Sampling station	Designation	Sampling station	Designation
Jornada		Curlew Valley	
Playa	P	*Artemisia tridentata*	
Bajada 1	B-1	dominated (Curlew 5)	CV-5
Bajada 2	B-2		
Bajada 3	B-3	*Ceratoides lanata*	
Silverbell	S	dominated (Curlew 6)	CV-6
Rock Valley	RV	*Atriplex confertifolia*	
Pine Valley	PV	dominated (Curlew 7)	CV-7

Soil Analyses - Chemical and Physical Factors

In order to chemically characterize the soils, the following analyses were performed.

Table 2. Collection periods

Site/Collection dates	Season designation
Jornada (playa and bajada):	
17 March 1975	Dry season, plants dormant
27 June 1975	Dry season, plants active
13 August 1975	Wet season, plants active
16 December 1975	Wet season, plants dormant
Silverbell:	
17 March 1975	Dry season, plants dormant
28 June 1975	Dry season, plants active
14 August 1975	Wet season, plants active
15 December 1975	Wet season, plants dormant
Rock Valley:	
4 April 1973	Wet season, plants active
21 March 1975	Wet season, plants dormant
29 July 1975	Dry season, plants active
12 December 1975	Dry season, plants dormant
Pine Valley:	
23 March 1974	Wet season, plants dormant
31 July 1975	Wet season, plants active
11 December 1975	Dry season, plants dormant
15 May 1976	Dry season, plants active
Curlew Valley	
2 January 1973	Wet season, plants dormant
26 March 1973	Wet season, plants dormant
17 April 1973	Wet season, plants active
16 July 1973	Dry season, plants active
29 October 1973	Dry season, plants dormant
10 June 1975	Dry season, plants active
15 March 1976	Dry season, plants dormant
20 April 1976	Wet season, plants active

Ammonium Nitrogen (Bremner 1965)

Total ammonium. Four grams of soil were weighed into a 500 ml round bottom boiling flask and 20 ml of 40 percent sodium hydroxide was added. This was then steam-distilled and the distillate collected in 5 ml of 2 percent boric acid solution to which two drops of Tashiro's indicator was added. The boric acid solution was then titrated to the end point with 0.01 N $KH(IO_3)_2$.

Exchangeable ammonium. Ten grams of soil were placed in a 125 ml Erlenmeyer flask and 50 ml 2 N KCl was added. After one hour on a shaker, the contents of this flask were filtered through No. 2 Whatman filter paper into a 100 ml volumetric flask. The contents of the second flask were then brought to volume with distilled water. An aliquot of this solution was pipetted into a Kjeldahl boiling flask and approximately 0.2 g MgO was added. This mixture was then steam-distilled and the distillate was collected in 5 ml of 2 percent boric acid solution to which two drops of Tashiro's indicator was added. The boric acid was then titrated with 0.01 N $KH(IO_3)_2$.

$$\text{Calculations: } \text{mg } NH_4^+ - N/\text{g} = \frac{\text{titrated} - \text{blank} \times \text{normality of acid} \times 14}{\text{grams of soil}}$$

Fixed ammonium. This value was obtained by subtracting exchangeable ammonium from total ammonium.

Soil Moisture Content

Ten grams of each soil sample were placed into tared weighing bottles and placed in a drying oven at 100°C. After three days, the

samples were removed, allowed to cool, and reweighed. The amount of weight loss was calculated as the number of grams of water per 100 g of soil.

Soil pH

Five grams of each soil sample were weighed into a 10 ml beaker and 5 ml of distille water was added. The contents were stirred and then allowed to set for ten minutes. The contents were then stirred again and the pH measured with a Beckman pH meter, using small electrodes.

Water Potential Measurement (Robinson and Stokes 1949, Lang 1967, Campbell and Gardner 1971, Wiebe et al. 1971, Brown and Van Haveren 1972)

Soil water potential was measured during respiration measurements using a Wescor, Inc., Model MJ55 psychrometric voltmeter with a Model C051 sample psychrometer, which operates on the principle of Peltier cooling. The instrument was calibrated with two salt solutions. A sodium chloride calibration curve was used for soils with water potential between 0 and -40 bars. For measuring extremely low potentials (as low as -800 bars) a lithium chloride standard calibration curve was used. Standard curves are found in Appendix Tables 26 and 27. The temperature of the chamber was first read and then that of the solution. Cooling time was 1.5 minutes.

Total Nitrogen, Organic Carbon, Nitrate, Salinity, and Soil Texture

Analyses of soils for total nitrogen, organic matter, nitrate, salinity, and soil texture were done by the USU Soil Texting Laboratory according to their prescribed methods.

Soil Analyses - Biological-Biochemical Factors

The following analyses were made to measure microbial biomass and activity in the soils.

Microbial Numbers

The dilution plate count method was used to determine number of microorganisms. This technique is most frequently used to determine viable cells in soil and may be used as a method for isolating microorganisms from soil. A 1 g soil sample was weighed into a flask containing 99 ml of sterile distilled water after which the flask was shaken vigorously. The suspension was diluted and a 1 ml aliquot of appropriate dilution was added to a plate and cooled agar poured onto it. The plate was rotated to mix and incubated at room temperature 5 to 7 days. Plates were then examined for colonies of aerobic bacteria, fungi, proteolytic organisms, and chitinolytic organisms. Plates were incubated for four weeks and then examined for celluolytic organisms.

Soil extract agar with glucose was used to culture total aerobic bacteria. The media contained the following ingredients:

Bacto Agar	15.0 g
K_2HPO_4	0.5 g
Soil Extract	100 ml
Tap Water	800 ml
Glucose(1% w/v)	100 ml

The glucose solution was sterilized separately then added to the sterilized medium. The pH was adjusted to 6.8-7.2 before the medium

was autoclaved. Soil extract was prepared by autoclaving 1000 g of garden soil with 1000 ml of tap water for 60 minutes. Ten grams of $CaCO_3$ was added, the mixture was stirred, and then filtered through a Buchner funnel fitted with double Whatman No. 5 filter paper until a clear solution was obtained. The filtrate was sterilized and stored in the refrigerator at $4^{o}C$.

Fungi were determined using Martin's Medium (Allen 1957) which is made up of the following ingredients:

Peptone	5.0 g
KH_2PO_4	1.0 g
$MgSO_4 \cdot 7H_2O$	0.5 g
Rose Bengal	0.33 g
Bacto Agar	20.0 g
Tap Water	900 ml
Glucose (10% w/v)	100 ml

The glucose solution was sterilized separately, then added to the medium after both were sterilized. The pH was adjusted to 6.8-7.2 before the medium was autoclaved. Streptomycin was weighed out under aseptic conditions and 0.399 g was dissolved in 10 ml sterile distilled water. This was stored in the refrigerator and 1.0 ml added to 1 liter of cooled media immediately before using.

Proteolytic organisms were determined by counting colonies surrounded by clear areas on the agar. The agar was soil extract agar with 10 percent (v/v) skim milk added.

Chitinolytic organisms were grown on soil extract agar in which the glucose was substituted with a volume of chitin suspension

containing 50 to 75 mg of chitin per 500 ml of media. Colonies surrounded by clear zones were counted.

The number of cellulolytic organisms was determined by counting clear zones around colonies grown on soil extract agar to which 50 ml of 10 percent sterile heavy cellulose suspension was added in place of glucose.

Soil Respiration (Elkan and Moore 1962)

Ten g of soil sample was placed in a 125 ml screw-capped Erlenmeyer flask with center well. One ml of 0.05 N $Ba(OH_2)$ solution was added to the center well. A blank containing no soil but 1 ml of $Ba(OH)_2$ solution in the center well was also prepared. The flasks were tightly capped and incubated in a 30^{o} shaking water bath for 90 minutes. Titration was carried out with 0.02 N HCl using one drop of phenolphthalein indicator until a clear solution was obtained. One ml of the untreated $Ba(OH)_2$ solution was also titrated to determine the normality of the standing solution.

Calculations:

starting meq = ml HCl for $Ba(OH)_2$ x 0.02 meq/ml

final meq = ml HCl for sample x 0.02 meq/ml

blank meq = ml HCl for blank x 0.02 meq/ml

Total meq CO_2 evolved = (starting meq - final meq) - blank meq

Before and at the end of each incubation, the water potential of each soil sample was measured. The average bar readings between the

beginning and the end was the approximate bar pressure of the sample during the reaction time. Respiration measurements were done in duplicate.

Dehydrogenase Activity (Casida et al. 1964)

Each soil sample was weighed into three sterile screw-capped tubes, 6 g per tube. To two of the tubes 2.5 ml sterile distilled water and 1.0 ml of 3 percent aqueous solution of 2,3,5-triphenyltetrazolium chloride were added. To the third tube (control) 3.5 ml sterile distilled water was added. The tubes were mixed thoroughly with a Vortex mixer and then incubated in a 30°C incubator for 24 hours.

Following incubation, the reaction in the tubes was stopped by adding 5 ml of 90 percent methanol. The samples were then filtered into a 100 ml volumetric flask through a Buchner funnel fitted with Whatman No. 5 filter paper. During this procedure, it was necessary to keep the sample wet at all times until extraction was complete to avoid air being drawn through the soil. The filtrate was brought up to volume and the absorbance was read on a Bausch and Lomb Spectronic 20 at 485 nm. The readings were referenced to a standard formazan curve which was prepared from serial dilutions of 2,3,5-triphenylformazan working standard solution containing 0.03 mg formazan/ml methanol.

Proteolytic Activity (Hoffman and Teicher 1957)

Ten grams of soil sample were placed in each of three 100 ml screw-capped volumetric flasks and 500 mg of calcium carbonate was

added to the soil and mixed in. The soil was then dampened with 1.5 ml toluene and allowed to stand for 15 minutes, after which 20 ml of a freshly prepared 2 percent solution of gelatin was added to two flasks and 20 ml distilled water to the other flask. After thoroughly shaking, the flasks were placed on a culture tube rotating apparatus in a 37°C incubator.

After 20 hours incubation, the flasks were removed from the incubator and brought to volume (the toluene above the mark) with 37°C distilled water. The contents were mixed and gravity filtered through a double filter paper consisting of Whatman No. 5 on the outside and Whatman No. 2 on the inside.

To assay for the amount of hydrolyzed gelatin, 5 ml of each filtrate and 5 ml of cupric phosphate suspension were placed in a centrifuge tube. This mixture was allowed to stand for 5 minutes with occasional shaking and then centrifuged at 7000 rpm for 5 minutes. The supernatant was decanted into photometer tubes and the absorbance read at 600 nm on a Bausch and Lomb Spectronic 20. Values obtained were refereneced to a standard curve.

The standard curve was made with portions of a 2 percent solution diluted 1:5 containing the appropriate amino acids by weight that make up gelatin. The 1:5 dilution represented 100 percent hydrolysis of gelatin.

The cupric phosphate suspension reagent was prepared as follows: Into 40 ml of sodium phosphate solution was stirred (68.5 g/ℓ) 20 ml of cupric chloride solution (28.5 g/ℓ). The mixture was centrifuged at 7000 rpm for 5 minutes. The supernatant was discarded and the

precipitate was washed twice by resuspending in 60 ml of sodium borate buffer (10.1 g/ℓ pH 8.9-9.2) and centrifuging after each washing. The washed precipitate was resuspended in 100 ml borate buffer. Six g of sodium chloride was added and the suspension mixed and stored in a glass-stoppered bottle. The suspension remained stable for 10 days.

ATP Concentration (McElroy 1947, Stanley and Williams 1969, and Utter 1972)

Two g of soil was placed in a 250 ml boiling flask and 25 ml of a 1:1 boiling solution of Tris buffer and 95 percent ethanol were added. The flask was placed on a high vacuum rotating evaporator so that it was partially submerged in a 55°C water bath. After 5 minutes, the contents of the flask were brought up to a 25 ml volume with ice cold Tris buffer. Then the soil extract was centrifuged for 10 minutes at 10,000 rpm to remove the soil particles. Aliquots of the extract were dispensed into test tubes, capped, and placed in an ice bath for immediate assay or stored at -10°C.

The luciferin-luciferase suspension was prepared by rehydrating a vial of firefly lantern extract (Sigma FLE-50 to 250) with distilled water. The vial was left to stand at room temperature for two hours and then stored at 4°C. The suspension was centrifuged at 10,000 rpm for 10 minutes to remove insoluble debris before use.

A standard stock solution was prepared initially by dissolving 10 mg of crystalline disodium ATP (Sigma) in 1000 ml Tris buffer (0.02 M, pH 7.75). The solution was capped and stored at -10°C and working standards were prepared by thawing and diluting stock solution with Tris buffer to the desired concentration. A standard curve of

concentration versus an integral of count sequence was plotted on log paper and unknowns determined by such a curve. Standards were counted with each sample determination.

A liquid scintillation spectometer, Packard Tri-carb Model 527, was used to determine light intensity. The settings included 1) one channel only, 2) amplification set at 10 percent, 3) discriminators set at 50-1000, 4) repeat mode used for 20 sequential counts, and 5) spectrometer used out-of-coincidence.

For the light intensity measurement, 1.8 ml of standard or soil extract ATP solution was pipetted into a glass liquid scintillation counting vial. At zero time, 0.2 ml of reconstituted enzyme was added and shaken. Then the vial was placed on the elevator of a liquid scintillation counter and lowered into the counting chamber. The first count was begun 15 seconds after the enzyme additions for 6 seconds with a 2 second interval between counts for printout.

A blank was made by adding 0.2 ml of enzyme to 1.8 ml of Tris buffer. In addition, a soil extract blank was made by counting 1.8 ml of extract alone and the integral of sequential counts was subtracted from the integral of the luminated samples.

Recovery of ATP from soil was determined by using ATP in the form of viable bacterial cells. A 1×10^{-2} dilution of soil was inoculated by the spread plate method onto a plate of solidified soil extract agar. After incubation overnight in a $30^{o}C$ incubator, cultures were inoculated into a 10 percent nutrient broth shake culture and incubated overnight at room temperature. The cells were harvested by centrifugation and resuspended in 10 ml of sterile distilled water.

ATP was determined by extracting 1 ml of cell suspension following extraction procedures for soil samples. Prior to extracting soil samples, 1 ml of cell suspension was added to each soil sample and percent recovery was calculated by the following formula:

$$\frac{\text{(Soil + Internal Standard)ATP - Soil ATP}}{\text{Internal Standard ATP}} \times 100 = \%\ \text{ATP recovery}$$

Nitrification Potential (Lees and Quastrel 1946, Collins and Sims 1956)

Nitrification potential *in vitro* was measured by a perfusion method as follows. Vinyl acetate maleic acid copolymer (VAMA), a soil conditioner, was added to a 70-80 g soil sample (0.2 percent per weight of dry soil). Enough distilled water was added to bring the mixture to a smooth paste consistency. The paste was then sieved to obtain 2-5 mm crumblike particles and dried for two days.

After drying, 30 g of stabilized soil was placed in a perfusion flask containing 250 ml of water. Each sample was done in triplicate in order to have two experimental units and one control for each sample. The samples were perfused for 24 hours, after which the water in the experimental flasks was discarded and replaced with 250 ml of 0.01 M $(NH_4)_2SO_4$ (2.333 mg NH_4^+-N/g). The samples were then perfused for 20 days. The trials were run at 22°C in the dark with the soil under conditions of optimal aeration and water saturation, but not water logged. A 5 ml perfusate sample was collected every two days. The perfusates were than analyzed colorimetrically for NH_4^+-N by Nesslerization (Allen 1957), for NO_2^--N by a sulfanilic acid-alpha-

naphtholamine reaction (Allen 1957), and for NO_3^--N by the 4-methyl-umbelliferone method (Skujins 1964).

Microbial Activities Responses to Moisture Availability

Adjusted Moisture Level Experiment

This experiment was conducted to find the threshold moisture necessary to stimulate microbial activity in desert soils.

Soils collected in the months of June or July from all ten aforementioned sites were used in this experiment. The amount of added water necessary to bring these soils to field capacity (-0.3 bar) was determined. Respiration, dehydrogenase, and ATP concentration were measured at original field moisture. The soils were weighed into flasks or tubes in which the experiment was conducted and the soil moisture was adjusted to field capacity, 2/3 field capacity, 1/2 field capacity, 1/6 field capacity, and air dried. After adjusting each moisture level, the soil samples were allowed to incubate for 24 hours in the dark with the containers loosely capped. After the 24 hour incubation, the soils were analyzed for dehydrogenase activity, respiration, and ATP concentration. Respiration was run in triplicate and dehydrogenase and ATP concentration was run in duplicate. Water potential was measured one hour after respiration experiments to allow the soil temperatures to equilibrate to room temperature.

Adjusted Moisture Level Plus Added Organic Matter Experiment

This experiment was conducted to test the response of microorganisms to additions of readily utilizable organic matter in soil

adjusted to different moisture levels. Soils collected from Playa, Bajada 1, Rock Valley, and Curlew 7 in June or July 1975 were used in this experiment. These four soils were selected because of their organic carbon content. Playa and Curlew 7 were highest in organic carbon content and Bajada 1 and Rock Valley were lowest in organic carbon content. Selection of the soils from different deserts by these criteria was necessary in order to compare the response between soils high and low in organic carbon.

A sufficient amount of soil to measure respiration and dehydrogenase at five moisture levels was weighed into 400 ml beakers and a 1 percent w/w amount of glucose was added. The soil and glucose were well mixed and enough water added to completely moisten the mixture. The wet soils were quick-frozen in dry ice and acetone and then lyophilized for 24 hours. The lyophilized soils were removed from the beakers and mixed in a mortar with pestle. Respiration and dehydrogenase were measured in the lyophilized soils. The amount of added water necessary to bring the soil moisture level to field capacity was also determined. The soils were then moistened to 1/2 field capacity, 1/4 field capacity, 1/6 field capacity, and 1/12 field capacity. Respiration and dehydrogenase were measured at each moisture level. Respiration was run in triplicate and dehydrogenase was measured in duplicate. Only half the amount of soil designated in the procedure above was used at the higher moisture levels. Water potential measurements were taken one hour after the respiration measurements.

Drying Experiment

The purpose of this experiment was to observe the effect of drying on microbial activity in desert soils.

Soils collected in March 1975 or March 1976 from all ten sampling stations within the five desert sites were used in this experiment. Enough soil to measure respiration, dehydrogenase and ATP concentration at 6 drying intervals was weighed out and the soil was spread 1-2 cm deep in a 22.5 cm aluminum pan. The amount of added water necessary to bring the soils to field capacity was determined. Respiration, dehydrogenase, and ATP concentration were measured in the soil at original field moisture. The soils in the aluminum pan were moistened to field capacity and then allowed to air dry. Respiration, dehydrogenase, and ATP concentration were measured at field capacity, 24 hours after drying, 96 hours after drying, and 192 hours after drying. After the 192-hour drying period the soils were placed in a $30^{o}C$ incubator for 24 hours and respiration, dehydrogenase, and ATP concentration were again measured. The soils were then placed in a $37^{o}C$ incubator for 24 hours and respiration, dehydrogenase, and ATP concentration were then measured. Water potential at each interval was measured before and one after after respiration measurements. In order to determine nonbiological CO_2 evolution at each interval, soil was weighed into a respiration flask and the open flask placed in a desiccator with an open petri dish containing 20 ml propylene oxide. The desiccator was sealed and evacuated and the propylene oxide was allowed to saturate the soil for 22 hours. This was the predetermined time which resulted in sterilization of the soil.

Wetting-Drying Experiment

This experiment sought to simulate wetting and drying cycles in the desert and observe their effect on microbial activity.

Soils collected from all ten stations at the five desert sites during June or July 1975 were used in this experiment. Enough soil to measure respiration, dehydrogenase, ATP concentration, and total ammonium at four intervals was weighed into a 400 ml beaker. Casein (1% w/w) was added and mixed into the soil. Enough water was added to wet the soils thoroughly. The soils were quick-frozen in dry ice and acetone and then lyophilized for 24 hours. The lyophilized soil was analyzed for respiration, dehydrogenase, and ATP concentration. The amount of added water necessary to bring the soil moisture to field capacity was determined. The soils were moistened to field capacity and spread out 1-2 cm deep on a double thickness paper towel. The soils were analyzed at once for the aforementioned activities at field capacity and after eight days of air drying. The soil, air-dried for 8 days, was rewetted and analyzed for respiration, dehydrogenase, and ATP concentration.

Statistical Analysis

The field data collected in 1975 and the laboratory experiments were analyzed using analysis of variance, cluster analysis, and principal components techniques (Sneath and Sokal 1973). A correlation analysis between the activities was also run.

A three-way factorial analysis of variance (FCTCVR) program (found in STATPAC Library prepared by Rex Hurst, Department of Applied

Statistics and Computer Science, Utah State University, Logan) with a single replication was used to find significant differences between stations and between stations at different moisture seasons or moisture levels. The variables used to characterize the stations in the field analysis were respiration, dehydrogenase activity, ATP concentration, proteolytic activity, moisture content, nitrification potential, exchangeable ammonium, and nitrate content. The variables used the characterize the soils in the laboratory experiments were respiration, dehydrogenase activity, and ATP concentration.

Correlation analysis between selected pairs of activities was run using the revised multivariate data collection procedure (MDCR) program found in STATPAC Library prepared by Rex Hurst, Department of Applied Statistics and Computer Science, Utah State University, Logan.

The cluster analysis was run using the MINT numerical taxonomy computer written by F. James Rohlf (Department of Ecology and Evolution, SUNY, Stonybrook, New York). The options used in the cluster analysis were: 1) similarity index: average Euclidean distance, and 2) clustering method: unweighted pair-group arithmetic average clustering (UPGMA). The attributes of the ten sampling stations being clustered included respiration, dehydrogenase activity, proteolytic activity, ATP concentration, moisture content, water potential, salinity, pH, total ammonium, exchangeable ammonium, nitrate, nitrification potential, number of aerobic bacteria, number of fungi, total nitrogen, and organic carbon. Clustering where all attributes were used is referred to as the "All Attributes Cluster." These same attributes were used to run the principal components analysis. The purpose

of running these analyses was to determine similarities and dissimilarities between sampling stations based on these attributes.

Two other cluster analyses were run with different combinations of the aforementioned attributes. One combination included activities such as respiration, dehydrogenase, proteolytic activity, ATP concentration, water potential, and nitrification potential. This is referred to as the "Potential Activities Cluster." Another clustering approach used such attributes as soil status measurements which included organic carbon, total nitrogen, nitrate, total ammonium, salinity, and pH. This is referred to as the "Soil Status Cluster."

RESULTS

Soil Analysis at Different Collection Periods

The soils collected from four geographically separated deserts of the western United States during different moisture seasons exhibited fluctuations in microbial activity as measured by respiration, dehydrogenase activity, ATP concentration, proteolytic activity, and nitrification potential. Increases in microbial activity were a function of moisture fluctuations as modified by precipitation (see Figure 2). Microbial activity was also influenced by vegetation.

Table 3 gives the chemical analysis of soils collected from ten sampling stations located within five desert sites. Moisture content varied between sampling dates for each station; however, water content was not above 10.3 percent in any one soil at any collection time. Playa, Curlew 5, Curlew 6, and Curlew 7 had highest nitrogen and organic carbon content. Salinity of all soils was below 1.0 mmhos/cm and pH of all soils was less than 8.7. Curlew and Pine Valley soils were more alkaline than soils from other desert sites. All soils analyzed are sandy loams except Playa and Curlew soils which are clay loam and silt loam, respectively.

Microbial numbers are given in Table 4. For most collection dates, there are 10^6 aerobic bacteria per gram in all soils except Bajada 2 soils. There are 10- to 100-fold smaller numbers of fungi than aerobic bacteria in all soils. However, there are at least 10^5

Figure 2. Precipitation patterns given as monthly totals during years when soils were collected and analyzed for this study (Balph et al. 1974, MacMahon 1976, Turner 1976, Thames 1976, Whitford 1976).

JA - January
FE - February
MA - March
AP - April
MA - May
JU - June
JU - July
AU - August
SE - September
OC - October
NO - November
DE - December

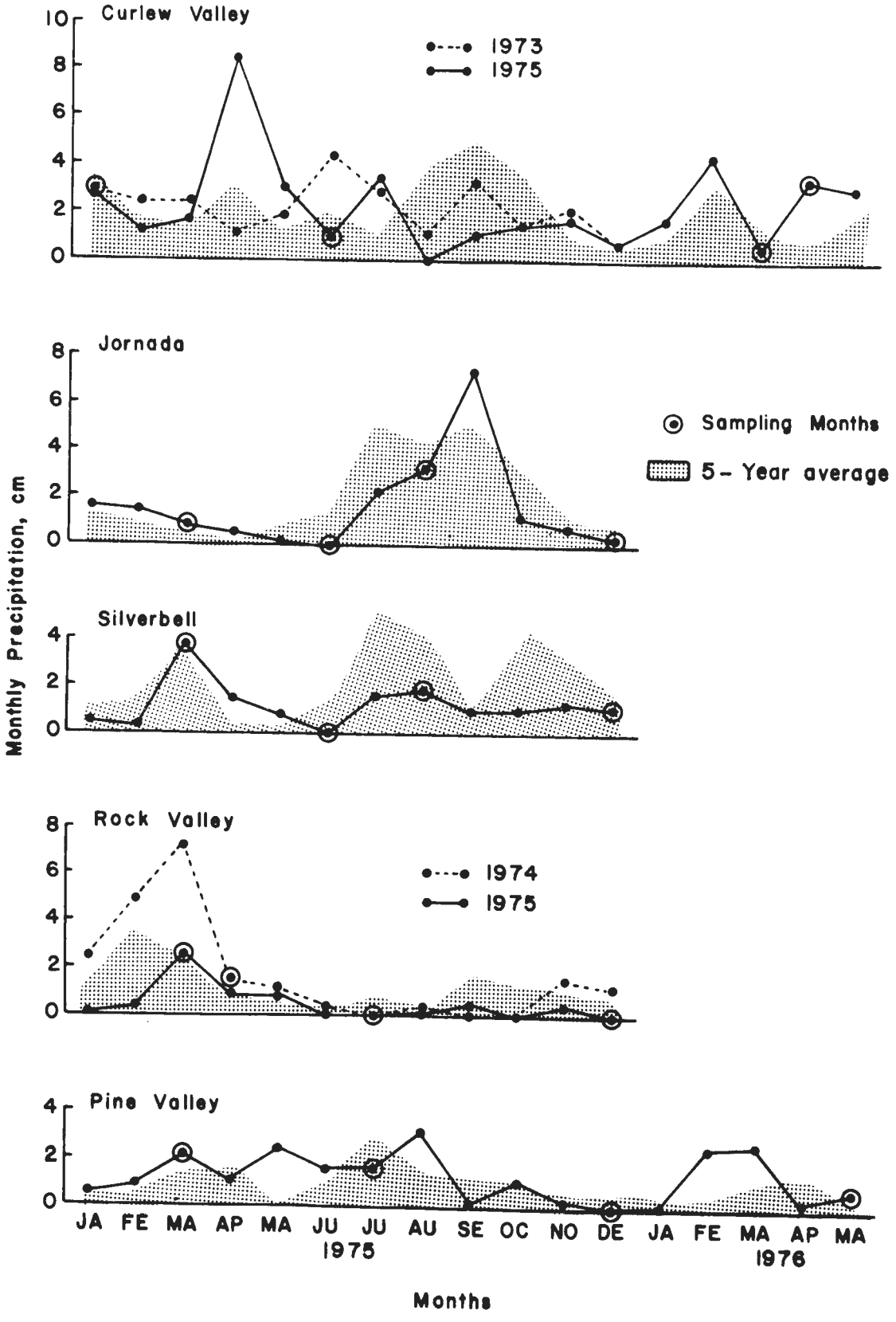

Curlew Valley
1973
1975
Jornada
Sampling Months
5 - Year average
Silverbell
Rock Valley
1974
1975
Pine Valley
Monthly Precipitation, cm
JA FE MA AP MA JU JU AU SE OC NO DE JA FE MA AP MA
1975
1976
Months

Table 3. Chemical analysis of soils

Sample/Sampling Date	Moisture Content % Water	Total N %	Org. C %	C/N Ratio	NO_3^- µg/g	ECe mmhos/cm	Fixed NH_4^+ µg/g	Exchang. NH_4^+ µg/g	pH	Texture Analysis		
										Soil	Mechanical Analysis	Soil Type
Playa - 3/75	10.0	0.17	1.53	9.0	11.0	0.7	98.3	2.6	7.6	P	21 47 32	Clay loam
6/75	5.1	0.16	1.36	8.5	14.9	0.9	102.4	4.2	7.7			
8/75	9.6	0.13	1.22	9.4	9.8	0.6	73.3	3.2	7.3			
12/75	7.6	0.10	0.82	8.2	3.6	0.6	75.7	2.9	8.1			
Bajada 1 - 3/75	0.8	0.04	0.24	6.0	0.8	0.5	13.7	0.8	7.5	B-1	77 11 12	Sandy loam
6/75	1.0	0.04	0.40	10.0	0.9	0.5	13.8	0.9	7.7			
8/75	1.5	0.03	0.30	10.0	0.9	0.3	11.7	1.5	6.5			
12/75	2.2	0.04	0.30	7.5	0.9	0.4	12.8	0.7	8.1			
Bajada 2 - 3/75	0.8	0.04	0.30	7.5	0.4	0.5	20.0	0.9	7.8	B-2	73 14 13	Sandy loam
6/75	0.9	0.04	0.41	10.3	0.8	0.4	11.6	1.5	8.1			
8/75	1.4	0.05	0.41	8.2	1.1	0.3	21.4	2.0	7.4			
12/75	3.1	0.04	0.35	8.8	1.6	0.4	20.2	1.5	8.0			
Bajada 3 - 3/75	1.4	0.05	0.40	8.0	0.6	0.5	17.9	0.9	7.5	B-3	73 15 12	Sandy loam
6/75	0.9	0.05	0.46	9.2	1.2	0.4	15.9	1.8	8.2			
8/75	1.4	0.04	0.34	8.5	1.2	0.3	12.3	2.0	7.9			
12/75	1.9	0.04	0.21	5.3	0.5	0.4	12.4	0.9	7.8			
Silverbell - 3/75	3.1	0.08	0.58	7.3	1.9	0.4	40.3	2.1	7.6	S	62 28 10	Sandy loam
6/75	0.8	0.05	0.52	10.4	2.0	0.4	23.2	3.2	6.5			
8/75	7.1	0.10	0.97	9.7	4.8	0.6	75.4	1.3	7.7			
12/75	6.5	0.12	1.14	9.5	18.3	0.9	56.4	2.4	7.7			
Rock Valley - 3/75	4.3	0.04	0.23	5.8	0.6	0.3	27.0	1.2	8.3	RV	70 28 10	Sandy loam
7/75	1.2	0.03	0.36	12.0	0.4	0.2	14.9	1.5	8.2			
12/75	2.3	0.04	0.30	7.5	1.6	0.3	13.2	0.8	8.1			
Pine Valley - 3/75	10.3	0.05	0.41	8.2	2.4	0.5	18.7	0.8	8.1	PV	23 28 10	Sandy loam
7/75	4.0	0.05	0.48	9.6	1.1	0.4	22.9	0.9	8.4			
12/75	2.1	0.06	0.60	10.0	1.8	0.4	23.6	0.9	8.3			
5/76	1.8	0.05	0.48	9.6	0.2	0.4	13.5	1.2	8.4			
Curlew 5 - 6/75	4.3	0.10	0.78	7.8	0.9	0.5	39.8	14.1	8.0	C5	32 55 13	Silt loam
3/76	5.3	0.11	1.08	9.8	0.5	0.5	36.2	1.2	8.2			
4/76	4.5	0.16	1.49	9.3	0.4	0.6	47.4	2.4	8.0			

Table 3. Continued

Sample/Sampling Date	Moisture Content % Water	Total N %	Org. C %	C/N Ratio	NO_3^- µg/g	ECe mmhos/cm	Fixed NH_4^+ µg/g	Exchang. NH_4^+ µg/g	pH	Texture Analysis		
										Soil	Mechanical Analysis	Soil Type
Curlew 6 - 6/75	2.5	0.11	0.90	8.2	0.8	0.7	22.3	1.8	8.1	C6	38 51 11	Silt loam
3/76	6.9	0.12	0.87	7.3	0.2	0.5	45.5	0.9	8.3			
4/76	4.3	0.14	1.11	8.0	0.2	1.2	32.8	2.4	8.0			
Curlew 7 - 6/75	5.3	0.10	0.98	9.8	0.7	1.0	32.7	1.3	8.1			
3/76	8.0	0.13	1.32	10.2	0.1	0.5	83.5	1.4	8.7			
4/76	4.5	0.15	1.54	10.3	0.5	3.4	58.1	2.5	8.0			

Table 4. Plate counts of aerobic bacteria, fungi, proteolytic organisms, chitinolytic organisms, and celluloytic organisms (coefficient of variation (C.V.) given for replicate plate counts)

Sample/Sampling Date	Aerobic Bacteria		Fungi		Proteolytic Organisms		Chitinolytic Organisms		Cellulolytic Organisms	
	# orgs/g	C.V.	# orgs/g	C.V.	# orgs/g	C.V.	# orgs/g	C.V.	# orgs/g	C.V.
Playa - 3/75	$8.5x10^6$	.37	$1.3x10^5$	.17	$1.8x10^7$	.24	$1.1x10^7$	.22	$1.3x10^4$	--
6/75	$4.6x10^7$	.24	$2.4x10^4$	.26	$2.1x10^6$	.17	$2.5x10^6$	.37	$4.1x10^6$	.22
8/75	$1.1x10^5$	.09	$5.9x10^5$	.16	$4.2x10^5$	.27	$1.2x10^6$	.14	$8.3x10^5$	.37
12/75	$4.6x10^5$	.09	$1.1x10^5$	.25	$4.9x10^5$	.30	$1.4x10^6$	.11	$2.1x10^5$	.11
Bajada 1 - 3/75	$5.0x10^5$	.10	$1.1x10^4$	.31	$1.8x10^5$	.16	$1.3x10^5$	.48	$4.8x10^4$	--
6/75	$1.9x10^6$	.20	$1.9x10^4$	.25	$3.3x10^4$	.34	$9.1x10^4$	.26	$1.4x10^6$	.24
8/75	$9.1x10^5$	.08	$1.8x10^4$	.31	$2.0x10^5$	.35	$1.0x10^5$	.31	$1.4x10^5$	.20
12/75	$6.0x10^5$	.14	$2.8x10^4$	.11	$1.2x10^5$	.25	$1.8x10^5$	.16	$1.1x10^5$	.30
Bajada 2 - 3/75	$2.7x10^5$	.18	$6.4x10^3$	.42	$9.3x10^4$	.24	$3.8x10^4$	.51	$1.0x10^5$	--
6/75	$7.2x10^5$	.20	$7.8x10^3$	.52	$2.5x10^3$	.94	$8.5x10^4$	.14	$1.2x10^5$	.50
8/75	$8.1x10^5$	.16	$5.5x10^3$	.45	$2.0x10^5$	.79	$1.9x10^4$	.46	$1.9x10^4$	.15
12/75	$4.4x10^5$	.18	$9.5x10^3$	.36	$1.5x10^5$	.24	$1.3x10^5$	.17	$7.3x10^4$	.11
Bajada 3 - 3/75	$2.3x10^6$	.34	$1.0x10^4$	.17	$1.5x10^5$	.38	$2.0x10^4$	.79	$1.1x10^5$	--
6/75	$2.3x10^6$	.05	$5.2x10^4$	.50	$9.2x10^4$	.33	$1.5x10^5$	.18	$2.1x10^5$	.31
8/75	$1.0x10^6$	.12	$2.0x10^4$	.48	$2.6x10^4$	.89	$7.3x10^4$	.39	$1.6x10^5$	.44
12/75	$3.7x10^5$	.15	$1.4x10^4$	.35	$7.9x10^4$	.25	$7.6x10^4$	.35	$1.1x10^5$	.16
Silverbell - 3/75	$3.3x10^6$	.31	$1.4x10^4$	.20	$2.9x10^5$	.42	$1.4x10^4$	.25	$1.1x10^4$	--
6/75	$2.9x10^6$	.24	$1.0x10^4$	.07	$9.7x10^4$	.47	$3.8x10^5$	.57	$1.8x10^6$	.42
8/75	$2.4x10^6$	.19	$1.8x10^4$	.16	$9.7x10^4$	.50	$2.5x10^5$	.17	$7.0x10^4$	.16
12/75	$1.4x10^6$	.34	$2.0x10^4$	.07	$3.6x10^5$	.13	$1.1x10^5$	.22	$7.6x10^4$	.38
Rock Valley - 3/75	$4.7x10^5$	.05	$6.3x10^3$	.63	$4.9x10^5$	.56	$6.3x10^3$	.29	$1.5x10^4$	--
7/75	$1.0x10^6$	.12	$5.4x10^3$	.81	$1.6x10^5$	.37	$5.9x10^4$	.35	$5.3x10^5$	.16
12/75	$5.2x10^5$	.17	$7.7x10^3$	.53	$1.9x10^5$	.24	$2.1x10^5$	.13	$6.4x10^4$	.23
Pine Valley - 3/75	$1.0x10^6$	.56	$5.1x10^3$	.25	$2.7x10^5$	.21	$5.1x10^3$	.23	$3.6x10^5$	--
7/75	$9.5x10^5$	.10	$3.5x10^3$	.26	$2.0x10^5$	.46	$1.3x10^5$	.19	$6.3x10^4$	.26
12/75	$7.5x10^5$	.09	$9.5x10^3$	.35	$1.9x10^5$	.30	$2.0x10^5$	.35	$9.3x10^4$	.10
5/76	$1.0x10^6$	.07	$4.8x10^3$	.39	$4.6x10^5$	.08	$3.7x10^5$	.12	$2.1x10^5$	.19
Curlew 5 - 6/75	--	--	--	--	$1.4x10^6$	--	$5.3x10^5$	--	$5.6x10^5$	--
3/76	$2.0x10^6$	.09	$2.3x10^4$	.17	$1.1x10^6$	.09	$5.9x10^5$	.15	$3.1x10^5$	.15
4/76	$7.3x10^5$	.06	$1.9x10^4$	.43	$6.2x10^5$	.25	$7.3x10^5$	.14	$3.5x10^5$	.09

Table 4. Continued

Sample/Sampling Date	Aerobic Bacteria		Fungi		Proteolytic Organisms		Chitinolytic Organisms		Cellulolytic Organisms	
	# orgs/g	C.V.	# orgs/g	C.V.	# orgs/g	C.V.	# orgs/g	C.V.	# orgs/g	C.V.
Curlew 6 - 6/75	--	--	--	--	$1.8x10^6$	--	$2.5x10^5$	--	$3.8x10^4$	--
3/76	$1.6x10^6$	.19	$1.6x10^4$	.31	$1.8x10^6$	.14	$5.5x10^5$	.18	$2.4x10^5$	.39
4/76	$6.8x10^6$	.47	$1.2x10^4$	.87	$5.7x10^5$	.14	$4.4x10^5$	.13	$3.5x10^5$	.11
Curlew 7 - 6/75	--	--	--	--	$1.1x10^6$	--	$3.2x10^5$	--	$7.8x10^5$	--
3/76	$5.5x10^6$	.17	$2.3x10^4$	.22	$1.1x10^6$	.29	$8.2x10^5$	.09	$4.8x10^5$	.12
4/76	$7.9x10^6$	.16	$2.8x10^4$	.24	$5.3x10^5$	.09	$4.9x10^5$	.14	$2.cx10^5$	.17

chitinolytic, proteolytic and cellulolytic organisms per gram in all soils except Bajada stations.

Raw data for dehydrogenase activity, respiration, ATP concentration, and proteolysis in soils collected for this study are given in Table 5.

The analysis of variance for eight soil parameters is given in Table 6 including those parameters indexing microbial activity, and two soil chemical constituents, exchangeable ammonium and nitrate, tested for ten soils and four dates combined. The significance level used in all the statistical comparisons in $P = 0.10$.

The analysis of variance shows that there is a significant difference among sampling stations for all parameters tested except ATP concentration, moisture content, and exchangeable ammonium. There is also a significant difference between seasons of active plant growth (designated "vegetative") and plant dormancy (designated "dormant") in respiration and proteolytic activity. Both proteolytic activity and respiration are significantly higher during the dormant seasons in all soils tested. Proteolytic activity and dehydrogenase activity are significantly higher during wet seasons. Seasonal moisture patterns were the major source of variation for nitrification potential. Greatest nitrification potential was found in soils collected during the dry season.

Table 7 gives mean and least significant difference (LSD) values for eight soil parameters for ten different soils. Playa, and Curlew 5, 6, and 7 soils are significantly higher than other soils tested in respiration for four dates combined, whereas Bajada 1, 2, and 3,

Table 5. Dehydrogenase activity, respiration ATP concentration and proteolysis in soils collected for this study (coefficient of variation (C.V.) given for replications)

Sample/Sampling Date	Dehydrogenase Activity (mg formazan/g)	C.V.	Respiration (μmoles/g/min)	C.V.	ATP† Concentration (μg/g)	C.V.	Proteolytic Activity (% hydrolysis)	C.V.
Playa - 3/75	.075	.03	26.7	.22	.0140	.24	7.0	.20
6/75	.056	.19	11.6	.23	.0190	.00	3.5	.00
8/75	.044	.22	9.7	.06	.0120	.23	5.0	.24
12/75	.049	--	31.4	.00	.0240	.03	6.1	.00
Bajada 1 - 3/75	.036	.06	10.1	.03	.0440	.18	3.0	.23
6/75	.037	.09	2.6	--	.0300	.02	4.0	.05
8/75	.021	.19	4.4	.22	.0380	.13	3.0	.22
12/75	.026	.09	15.3	.41	.0350	.18	8.2	.20
Bajada 2 - 3/75	.051	.00	10.5	.03	.0290	.19	7.0	.07
6/75	.038	.25	1.6	.23	.0230	.21	3.5	.23
8/75	.009	.03	8.3	.23	.0510	.23	3.0	.24
12/75	.014	.00	11.4	.05	.0360	.13	3.9	.00
Bajada 3 - 3/75	.024	.00	5.6	.23	.0240	.02	7.0	.00
6/75	.051	.00	6.7	.08	.0330	.24	5.5	.25
8/75	.010	.16	8.6	.02	.0270	.22	5.1	.25
12/75	.012	.06	6.3	.23	.0360	.22	12.5	.13
Silverbell - 3/75	.088	.08	7.6	.23	.0460	.21	8.0	.07
6/75	.061	.06	10.4	.00	.0240	.05	12.0	.07
8/75	.562	.23	6.7	.00	.5450	.21	22.0	.15
12/75	.030	.03	16.4	.16	1.1740	.10	23.0	.03
Rock Valley - 4/73	.101	.13	14.3	--	--	--	12.0	--
3/75	.047	.23	12.3	.06	.0390	.02	10.0	.18
7/75	.095	.04	5.6	.23	.0150	.05	11.6	.13
12/75	.078	.03	11.0	.03	.0560	.16	17.1	.11
Pine Valley - 3/75	.062	.23	18.3	.04	.1370	.15	3.0	.00
7/75	.081	.14	5.3	.22	.0120	.00	21.5	.04
12/75	.071	.19	4.1	.00	.0540	.05	14.2	.00
5/76	.034	.00	6.6	.44	.1030	.22	14.3	.08
Curlew 5 - 1/73	.413	.01	29.7	.11	--	--	31.0	--
6/75	.099	.03	11.4	.03	.0240	.14	18.8	.06
3/76	.072	.09	40.8	.02	.7330	.22	37.5	.00
4/76	.207	.01	7.0	.22	.0550	.23	25.5	.06

Table 5. Continued

Sample/Sampling Date	Dehydrogenase Activity (mg formazan/g)	C.V.	Respiration (µmoles/g/min)	C.V.	ATP† Concentration (µg/g)	C.V.	Proteolytic Activity (5 hydrolysis)	C.V.
Curlew 6 - 1/73	.032	.23	26.0	.10	--	--	20.0	--
6/75	.192	.04	5.2	.07	.0380	.14	17.5	.25
3/76	.068	.23	51.3	.00	.4140	.17	29.0	.00
4/76	.191	.14	7.5	.41	.0480	.23	23.8	.07
Curlew 7 - 1/73	.423	.19	33.6	.10	--	--	39.5	--
6/75	.164	.08	9.1	.18	.0540	.13	20.0	.25
3/76	.208	.23	36.5	.11	.4180	.23	33.0	.00
4/76	.436	.03	7.6	.22	.0430	.22	41.5	.12

† ATP recovery ranged from 28 to 82 percent.

Table 6. Factorial analysis of variance for eight soil parameters tested for ten sampling stations and four dates combined

Source of Variation	df	Expected Mean Square and Significance							
		Resp.[1]	Dehydro.[2]	Proteo.[3]	ATP[4]	% Moist.[5]	NO_3^-[6]	NH_4^+[7]	Nitrif.[8]
Sampling station (S)	9	179.73*	.039*	424.12*	.070	94.57	.430*	5.013	97269.9*
Moisture (M)	1	12.21	.055*	116.62*	.001	248.00*	.006	5.919	10800.8*
Season of Higher Plant Growth (V)	1	726.76*	.002	122.85*	.077	204.30*	.007	9.604	202.6
S x M Interaction	9	31.99	.014	29.97	.099*	51.96	.147	4.576	40743.8*
S x V Interaction	9	200.71*	.008	20.65	.020	77.30	.056	5.985	681.1
M x V Interaction	1	86.73	.0003	21.26	.016	290.52*	.000	.025	7.0
S x M x V Interaction	9	73.50	.009	25.50	.037	39.83	.079	3.419	2563.2
Total	39								

[1] Respiration (Resp.) units = moles CO_2/g/min.
[2] Dehydrogenase (Dehydro.) units = mg formazan/g
[3] Proteolysis (Proteo.) units = % hydrolysis
[4] ATP concentration (ATP) units = µg/g
[5] Percent moisture(% Moist.) units = % water
[6] Nitrate (NO_3^-) units = mg/g
[7] Exchangeable NH_4^+ (Ex. NH_4) units = mg/g
[8] Nitrification Potential (Nitrif.) = total amount of nitrate accumulated per 20 days perfusion
* Significant at Alpha = 0.10

Table 7. Mean and LSD values for eight soil parameters tested for ten sampling stations and four dates combined

Stations	Resp.	Dehydro.	Proteo.	ATP	% Moist.	NO_3^-	Ex. NH_4^+	Nitrif.
P	19.85	0.056	5.40	0.017	8.1	0.98	3.3	512.4
B-1	8.10	0.036	4.55	0.038	1.4	0.09	1.0	5.3
B-2	7.95	0.028	4.35	0.035	1.6	0.10	1.8	4.1
B-3	6.80	0.024	7.53	0.030	1.4	0.09	1.6	16.4
S	10.80	0.198	16.25	0.447	4.4	0.68	2.5	142.5
RV	10.80	0.080	12.68	0.028	3.8	0.07	1.2	9.5
PV	8.58	0.062	13.25	0.077	4.6	0.14	1.2	7.0
C 5	22.53	0.200	28.20	0.203	12.7	0.05	4.5	79.1
C 6	22.38	0.188	22.58	0.125	12.4	0.03	1.3	36.6
C 7	21.70	0.308	33.50	0.129	13.2	0.04	1.6	51.1

$LSD_{0.10}$ Respiration (Resp.) = 11.11
Dehydrogenase (Dehydro.) = 0.123
Proteolysis (Proteo.) = 6.55
Nitrate (NO_3^-) = 0.36
Nitrification Potential (Nitrif.) = 65.6

Silverbell, Rock Valley, and Pine Valley are similar to each other in respiration for four dates combined. Dehydrogenase activity is significantly higher in Curlew 5, 6, and 7 and Silverbell soils than in other six soils but dehydrogenase activity is not significantly different between Curlew and Silverbell soils. Nitrate content and nitrification potential are highest in Playa soils. Curlew soils have significantly higher moisture content than soils from other stations for four dates combined. Table 8 gives mean and LSD values for ATP concentration tested for wet and dry seasons and ten sampling stations combined.

Table 9 gives mean and LSD values for nitrification tested for wet and dry seasons and ten sampling stations combined. Table 10 gives mean and LSD values for respiration tested for vegetative and dormant seasons and ten sampling stations combined. During the wet seasons, nitrification is highest in Playa soil and there is no significant difference in nitrification potential between the other nine soils. During the dry season, however, Playa and Silverbell soils are significantly different in nitrification potential from the other eight soils but are not significantly different from each other.

Respiration does not differ significantly among sampling stations during the "vegetative" season (Table 10). However, respiration differs significantly among stations in the "dormant" season.

Selected paired activities that showed significant correlation are given in Table 11. Nitrate and nitrification potential showed the strongest correlation.

Table 8. Mean and LSD values for ATP concentration tested for wet and dry seasons and ten sampling stations combined

Sampling stations	ATP concentration[†]	
	Dry	Wet
P	0.017	0.018
B-1	0.037	0.037
B-2	0.026	0.044
B-3	0.029	0.032
S	0.035	0.860
RV	0.027	0.028
PV	0.075	0.079
C5	0.379	0.028
C6	0.226	-.024
C7	0.236	0.022

$LSD_{0.10}$ = 0.351

[†]ATP concentration units = µg/g

Table 9. Mean and LSD values for nitrification potential tested for wet and dry seasons and ten sampling stations combined

Sampling Stations	Nitrification Potential†	
	Wet	Dry
P	797.91	226.86
B-1	3.30	1.20
B-2	1.30	2.60
B-3	18.41	14.38
S	35.77	249.27
RV	17.14	1.90
PV	7.54	6.51
C 5	43.29	115.05
C 6	46.30	26.83
C 7	53.17	49.03

$LSD_{0.10}$ = 92.80

†Nitrification expressed as total amount of nitrate accumulation per 20 days incubation.

Table 10. Mean and LSD values of respiration for vegetative and dormant seasons across ten stations combined

Sampling Stations	Respiration†	
	Vegetative	Dormant
P	18.20	21.50
B-1	7.25	8.95
B-2	9.40	6.50
B-3	7.10	6.50
S	8.10	13.50
RV	11.65	9.95
PV	11.20	5.95
C 5	9.20	35.25
C 6	6.10	38.65
C 7	8.35	35.05

$LSD_{0.10} = 15.72$

†Respiration expressed as rate of CO_2 evolution.

Table 11. Correlation coefficients between selected paired activities measured in collected soils

Activities Correlated	$r = \frac{\Sigma(x-\bar{x})(y-\bar{y})}{\sqrt{2(x-\bar{x})^2\Sigma(y-\bar{y})^2}}$ [†]
Respiration - ATP	.38
Respiration - Proteolysis	.50
Respiration - Moisture Content	.54
Dehydrogenase - Proteolysis	.69
Dehydrogenase - Moisture	.61
Proteolysis - ATP	.39
ATP - Nitrate	.45
Proteolysis - Moisture Content	.45
Nitrate - Nitrification Potential	.79

[†] Significant at alpha = 0.05, from Snedecor and Cochran (1967).

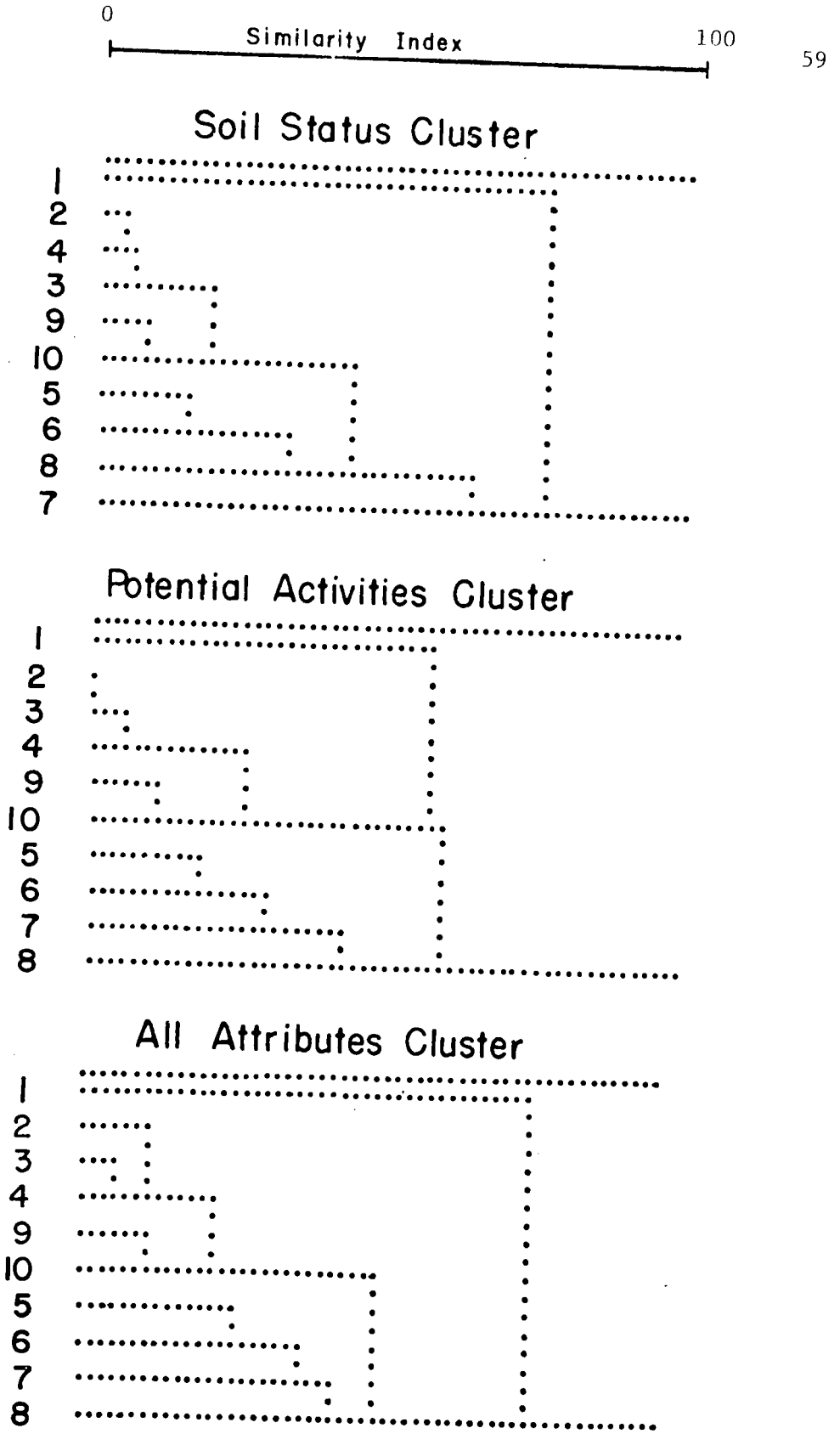
The cluster analysis phenograms are shown in Figure 3. The bottom of the tree corresponds to the start (first clustering cycle) where each individual is a separate cluster. The formation of clusters is defined by horizontal lines within the tree. The individuals contained within a cluster are defined by locating a horizontal line and then tracing all connected lines back to the bottom of the tree. The greater the height of the horizontal line as measured from the bottom of the tree--given by a similarity index scale with larger values denoting less similarity--the less is the similarity between the two joining clusters.

From the "All Attributes Cluster" it can be concluded that playa (Jornada) is the most distinct station and Bajada 2 and Bajada 3 are most similar. HAwever, two clusters can be picked out, with playa being by itself. The clusters seem to be Bajada 1, 2, and 3, Rock Valley, and Pine Valley, and Curlew 5, 6, and 7 and Silverbell. The same clusters are discerned in the "Soil Status Cluster" and the "Potential Activities Cluster." These conclusions are based on the location of the horizontal line chosen on the tree and the attributes used to characterize each individual being clustered.

The principal components analysis using the attributes in the "All Attributes Cluster" showed that 89 percent of the variability between sampling stations was due to respiration, dehydrogenase activity, and ATP concentration.

Figure 3. Phenograms of three cluster analyses, All Attributes Cluster, Potential Activities Cluster, and Soil Status Cluster.

Code: Number on tree	Sampling station
1	Playa
2	Bajada 1
3	Bajada 2
4	Bajada 2
5	Curlew 5
6	Curlew 6
7	Curlew 7
8	Silverbell
9	Rock Valley
10	Pine Valley


0
Similarity Index
100
Soil Status Cluster
1
2
4
3
9
10
5
6
8
7
Potential Activities Cluster
1
2
3
4
9
10
5
6
7
8
All Attributes Cluster
1
2
3
4
9
10
5
6
7
8

Nitrification Potential

The analysis of variance for the soil analysis reported in the previous section included nitrification potential and summarized the comparison of seasons and sampling stations. When increase of nitrite and nitrate are plotted graphically against time the growth rate of the nitrifying bacteria and the response of nitrifying organisms to added ammonium are exhibited.

Figures 4, 5, and 6 show the nitrification potential of added ammonium substrate in ten different soils. (Raw data are found in Appendix Table 28). Playa soil shows the highest accumulation of nitrate although nitrite level rises quite high before it begins to decrease. Curlew 5, 6, and 7 soils behave similarly, all showing high nitrite accumulation above that of nitrate (Figures 4 and 6).

Bajada 1, Bajada 2, and Pine Valley soils show no nitrate accumulation in 20 days of incubation (Figures 4 and 5). Only Silverbell soils have a higher nitrate accumulation than nitrite.

Figures 7 through 14 show seasonal comparison of nitrification potential for each sampling station (raw data are found in Appendix Tables 28 through 35). Playa soils have the highest accumulation of nitrate in March and August soils (Figure 7). Nitrite level is higher than nitrate in soils collected at all dates. Bajada 1 soils show very little nitrification potential (Figure 8). August and December samples show a lag period of 16 to 20 days for any nitrate increase.

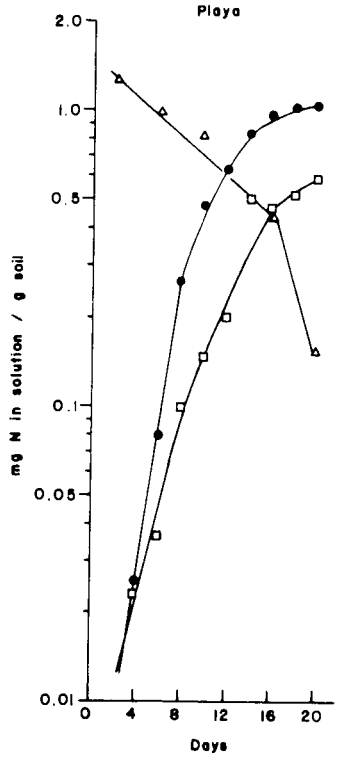
Similarly, Bajada 2 soils show little if any nitrate increase (Figure 9). Of the Bajada stations, Bajada 3 is the only one which shows any nitrate accumulation, although it is relatively low (Figure 10).

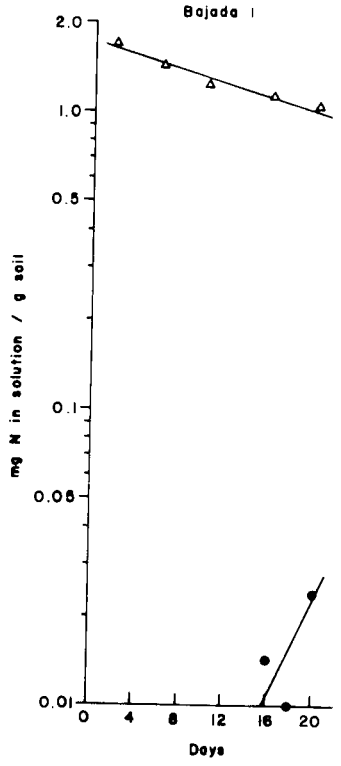
Figure 4. Nitrification potential of Playa, Bajada 1, Bajada 2, and Bajada 3 samples (March, June, August, and December averaged).

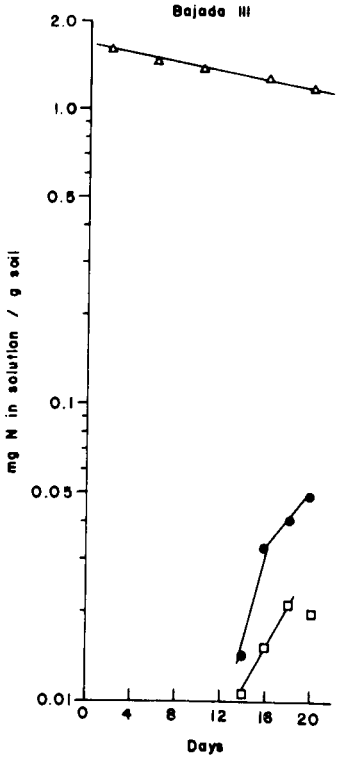
Δ - NH_4^+-N

● - NO_2^--N

□ - NO_3^--N


Playa
2.0
1.0
0.5
0.1
0.05
0.01
mg N in solution / g soil
0
4
8
12
16
20
Days


Bajada I
2.0
1.0
0.5
0.1
0.05
0.01
mg N in solution / g soil
0
4
8
12
16
20
Days


Bajada III
2.0
1.0
0.5
0.1
0.05
0.01
mg N in solution / g soil
0
4
8
12
16
20
Days

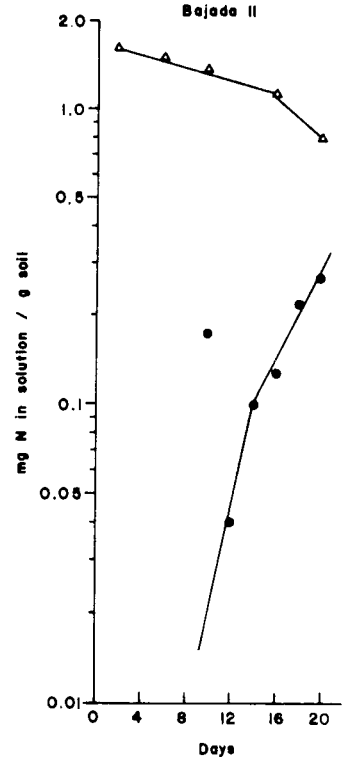
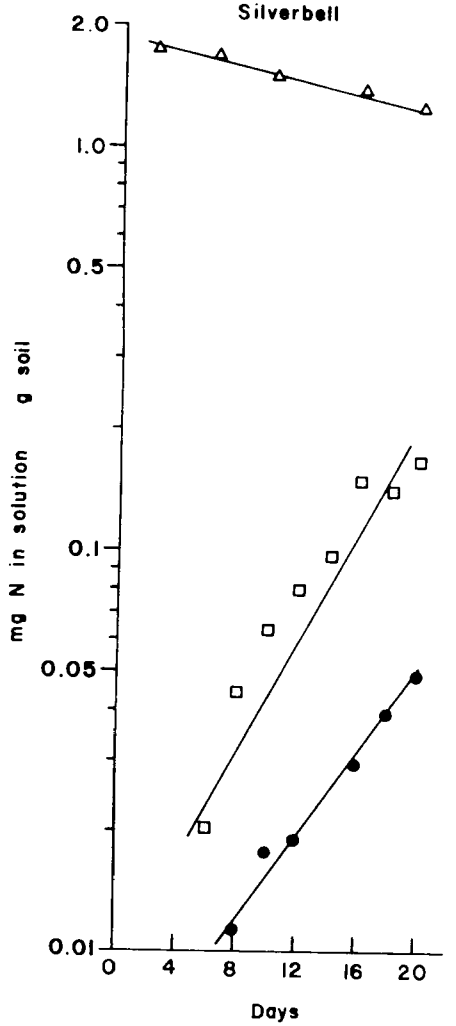

Bajada II
2.0
1.0
0.5
0.1
0.05
0.01
mg N in solution / g soil
0
4
8
12
16
20
Days

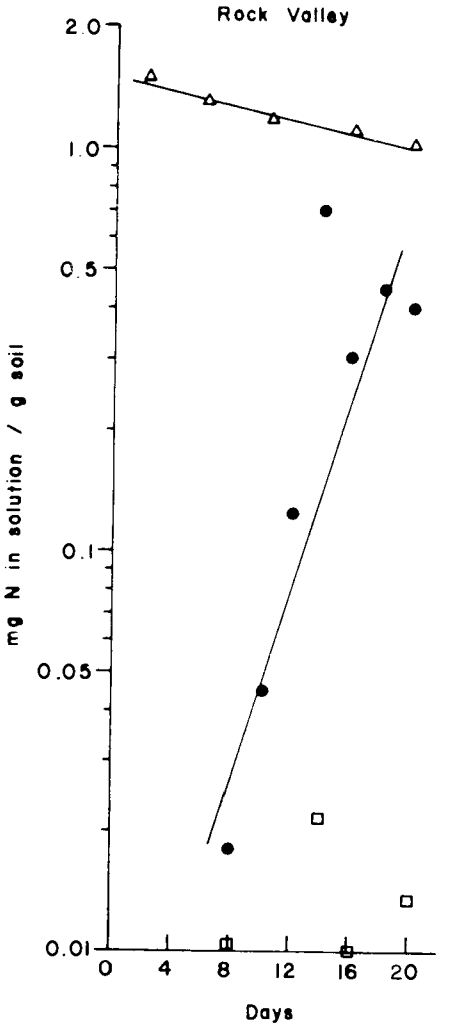
Figure 5. Nitrification potential of Silverbell samples (March, June, August, and December averaged), Rock Valley samples (March, July, and December averaged) and Pine Valley samples (March, July, December and May averaged).

Δ - NH_4^+-N

● - NO_2^--N

□ - NO_3^--N


Silverbell
2.0
1.0
0.5
0.1
0.05
0.01
mg N in solution g soil
0
4
8
12
16
20
Days


Rock Valley
2.0
1.0
0.5
0.1
0.05
0.01
mg N in solution / g soil
0
4
8
12
16
20
Days

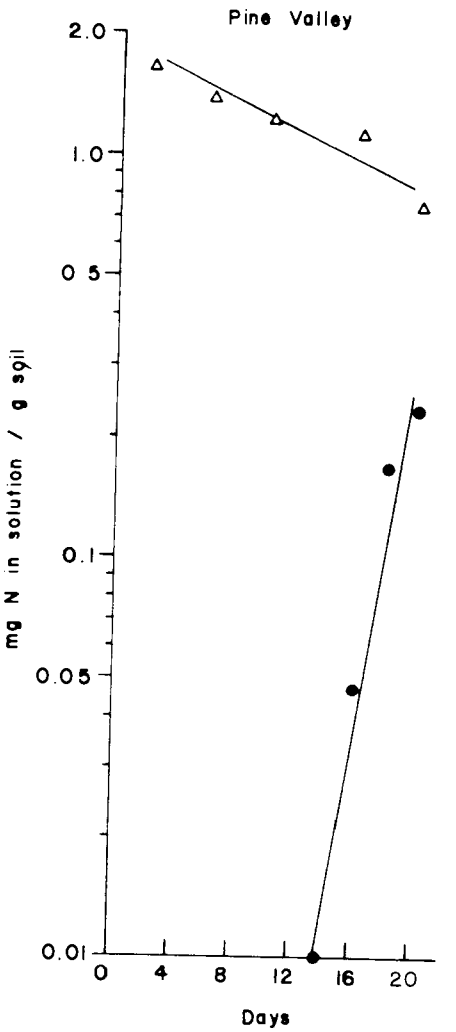
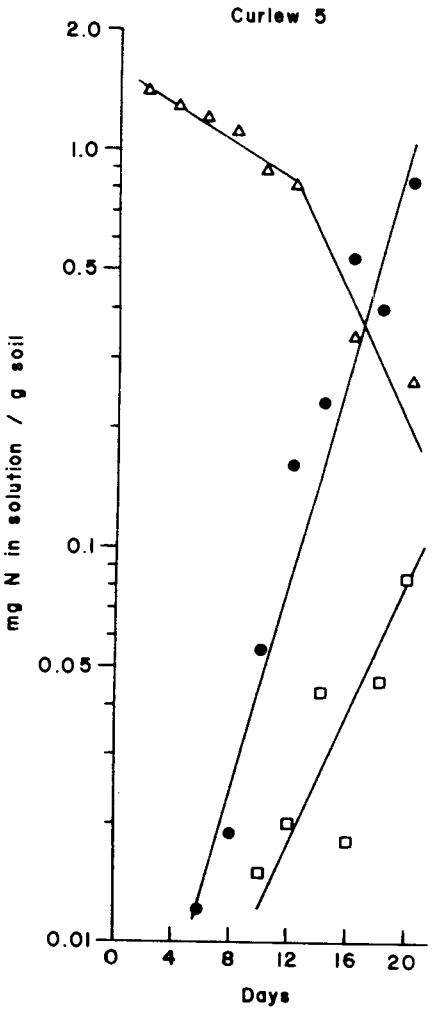

Pine Valley
2.0
1.0
0 5
0.1
0.05
0.01
mg N in solution / g soil
0
4
8
12
16
20
Days

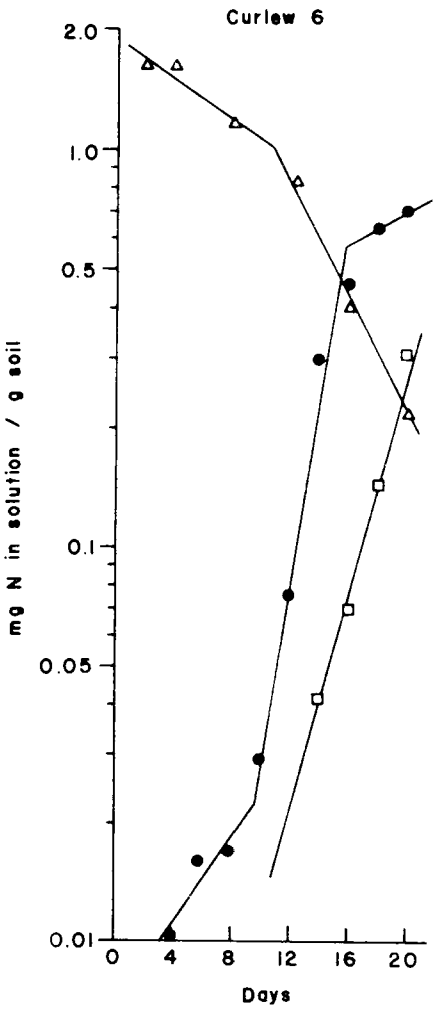
Figure 6. Nitrification potential of Curlew 5, Curlew 6, and Curlew 7 stations, all months averaged.

Δ - NH_4^+-N

● - NO_2^--N

□ - NO_3^--N


Curlew 5
mg N in solution / g soil
2.0
1.0
0.5
0.1
0.05
0.01
0
4
8
12
16
20
Days


Curlew 6
mg N in solution / g soil
2.0
1.0
0.5
0.1
0.05
0.01
0
4
8
12
16
20
Days

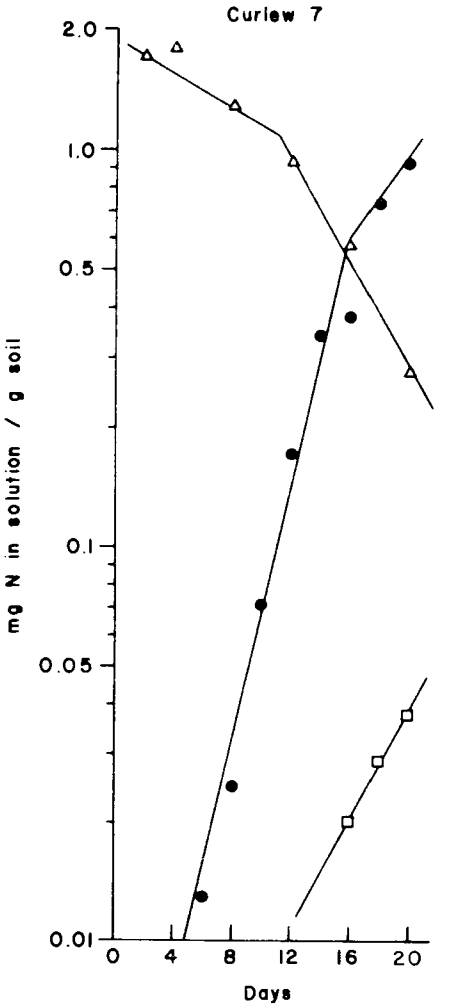
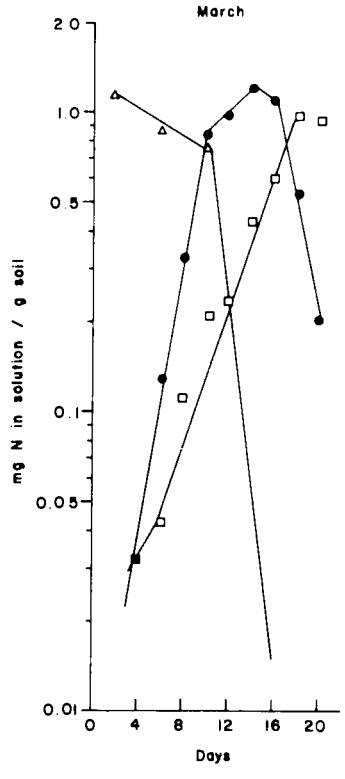

Curlew 7
mg N in solution / g soil
2.0
1.0
0.5
0.1
0.05
0.01
0
4
8
12
16
20
Days

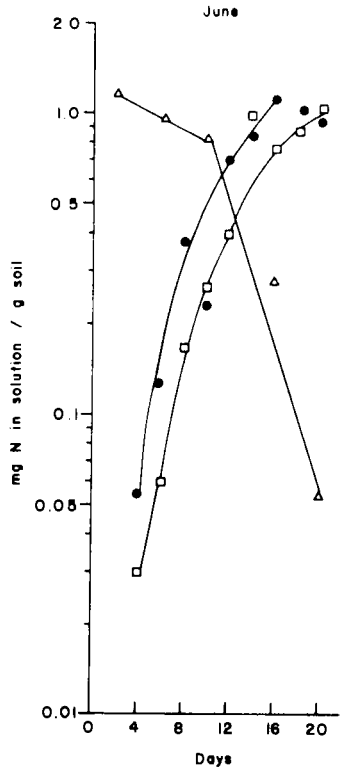
Figure 7. Date comparison of nitrification potential in playa soils average of duplicate samples.

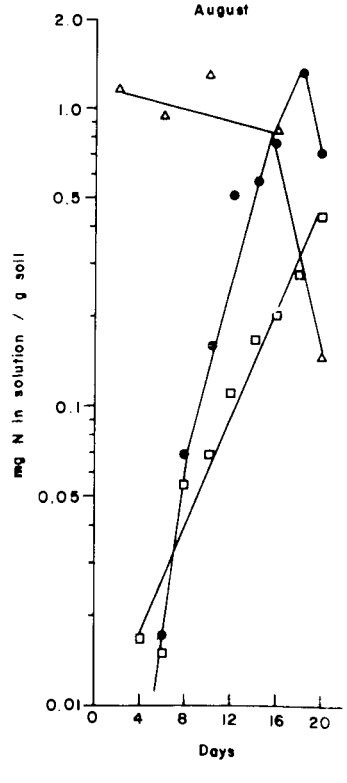
Δ - NH_4^+-N

● - NO_2^--N

□ - NO_3^--N


March
2.0
1.0
0.5
0.1
0.05
0.01
mg N in solution / g soil
0
4
8
12
16
20
Days


June
2.0
1.0
0.5
0.1
0.05
0.01
mg N in solution / g soil
0
4
8
12
16
20
Days


August
2.0
1.0
0.5
0.1
0.05
0.01
mg N in solution / g soil
0
4
8
12
16
20
Days

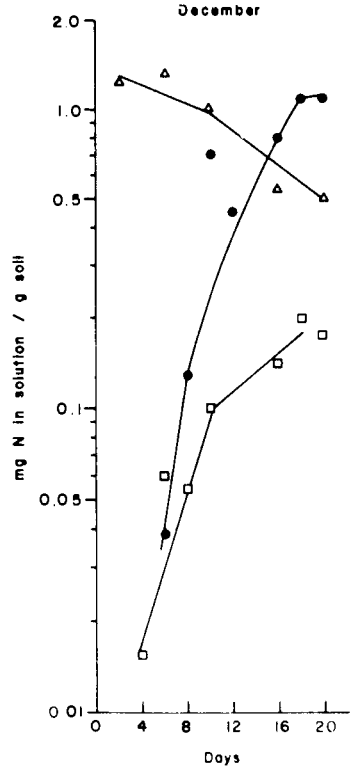

December
2.0
1.0
0.5
0.1
0.05
0.01
mg N in solution / g soil
0
4
8
12
16
20
Days

Figure 8. Date comparison of nitrification potential in Bajada 1 soils, average of duplicate samples

Δ - NH_4^+-N

● - NO_2^--N

□ - NO_3^--N

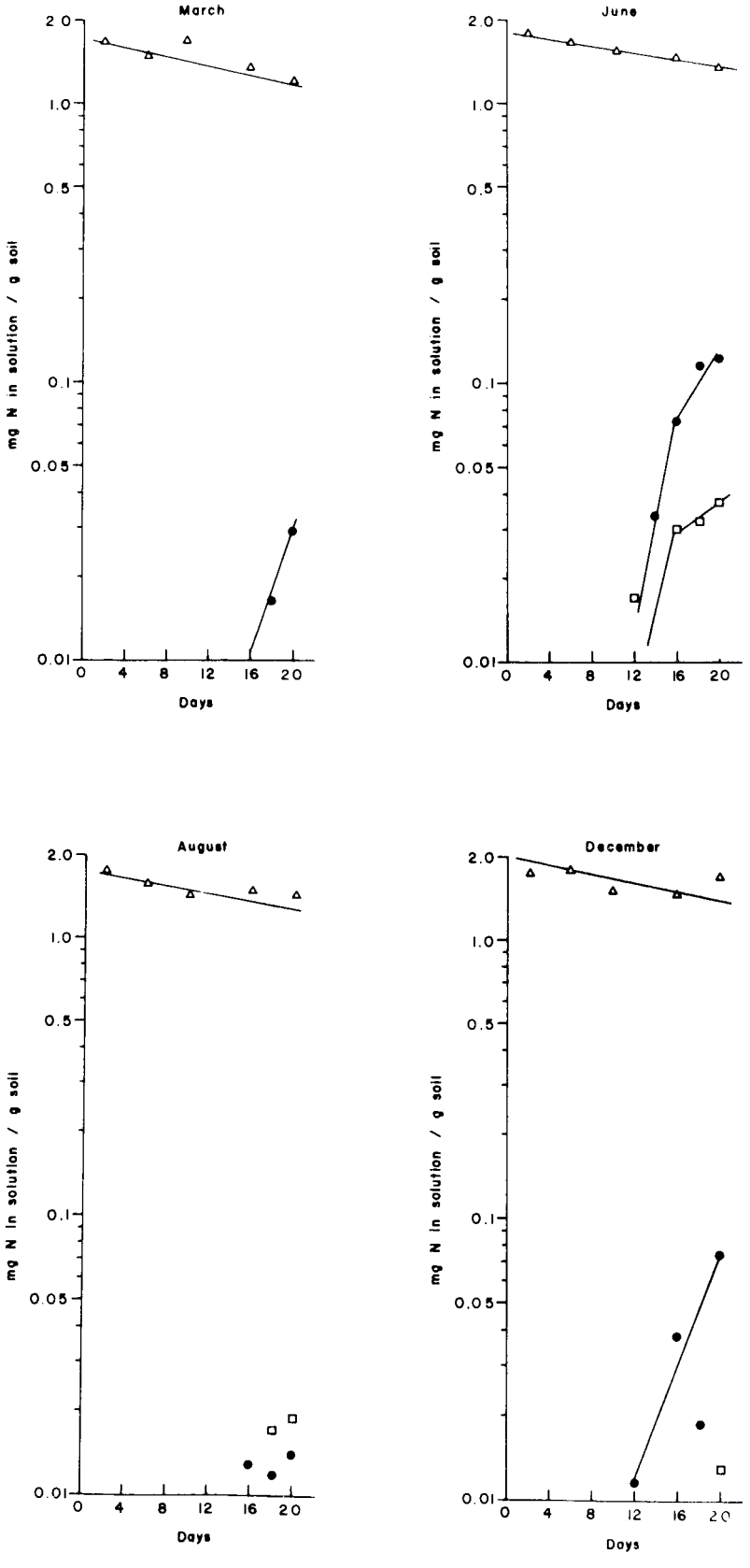

March
June
August
December
mg N in solution / g soil
Days
2.0
1.0
0.5
0.1
0.05
0.01
0
4
8
12
16
20

Figure 9. Date comparison of nitrification potential in Bajada 2 soils, average of duplicate samples.

Δ - NH_4^+-N

● - NO_2^--N

□ - NO_3^--N

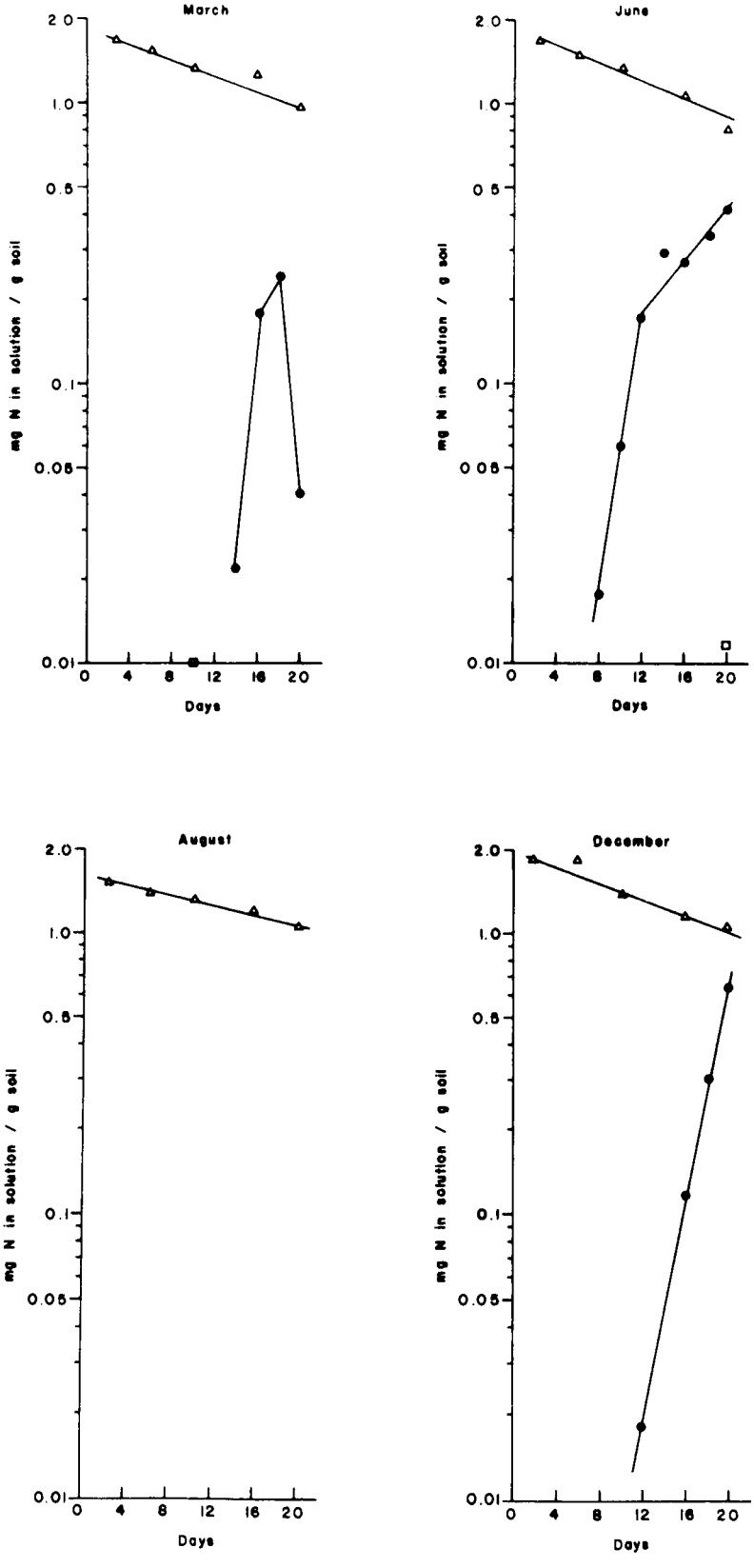
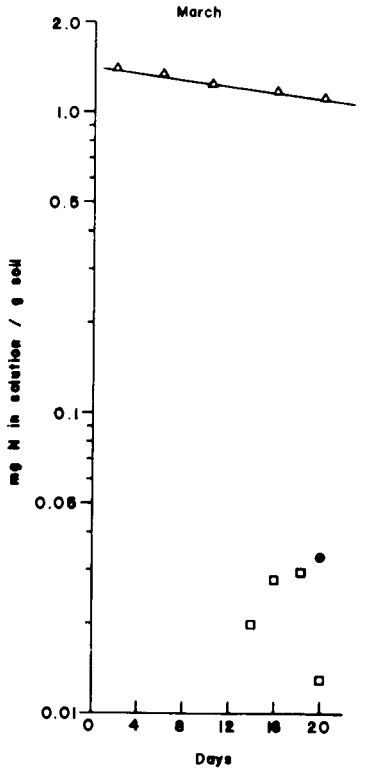

March
June
August
December
mg N in solution / g soil
Days
2.0
1.0
0.5
0.1
0.05
0.01
0
4
8
12
16
20

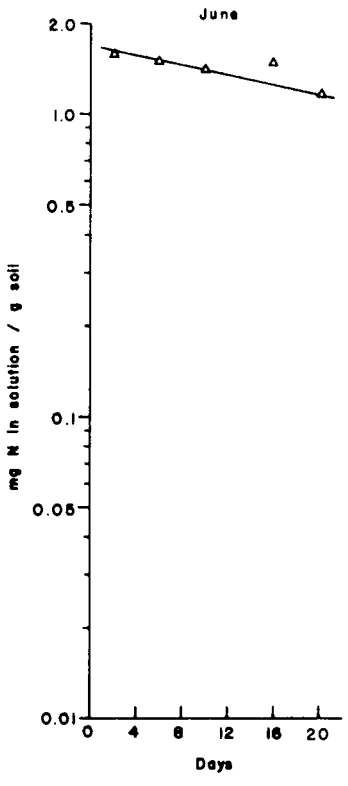
Figure 10. Date comparison of nitrification potential in Bajada 3 soils, average of duplicate samples.

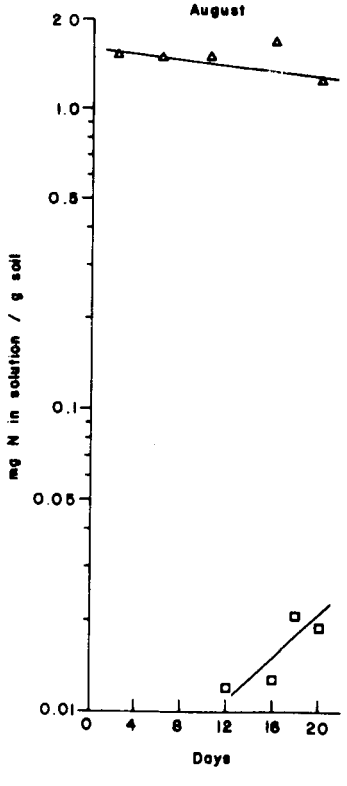
Δ - NH_4^+-N

● - NO_2^--N

□ - NO_3^--N


March
2.0
1.0
0.5
0.1
0.05
0.01
mg N in solution / g soil
0
4
8
12
16
20
Days


June
2.0
1.0
0.5
0.1
0.05
0.01
mg N in solution / g soil
0
4
8
12
16
20
Days


August
2.0
1.0
0.5
0.1
0.05
0.01
mg N in solution / g soil
0
4
8
12
16
20
Days

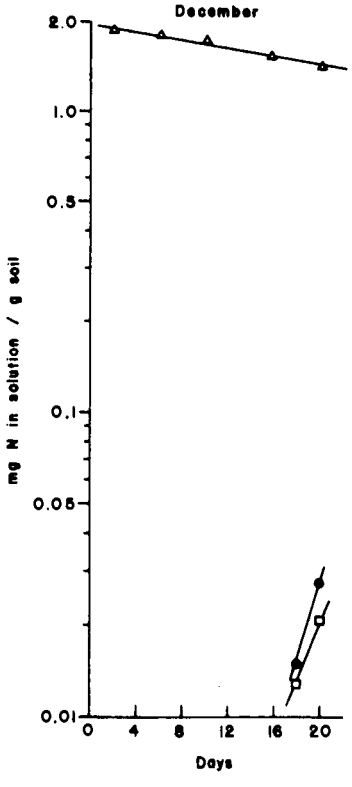

December
2.0
1.0
0.5
0.1
0.05
0.01
mg N in solution / g soil
0
4
8
12
16
20
Days

Figure 11 shows nitrification potential of Silverbell soils. In March and August samples there is no nitrite accumulation and December samples have the greatest nitrification potential whereas June samples have the lowest.

Rock Valley soils have little nitrification potential (Figure 12). Both ammonium and nitrite oxidizers show little if any potential activity in July samples.

Nitrification potential for Pine Valley soils is shown in Figure 13. Both July and December soils show negligible nitrate accumulation and March and May soils show some nitrification potential.

Finally, Figure 14 shows average nitrification potential of Curlew soils, stations 5, 6, and 7. March and April samples show the greatest nitrification potential and October samples show the lowest. July samples have the greatest nitrite accumulation.

Adjusted Moisture Level Experiment

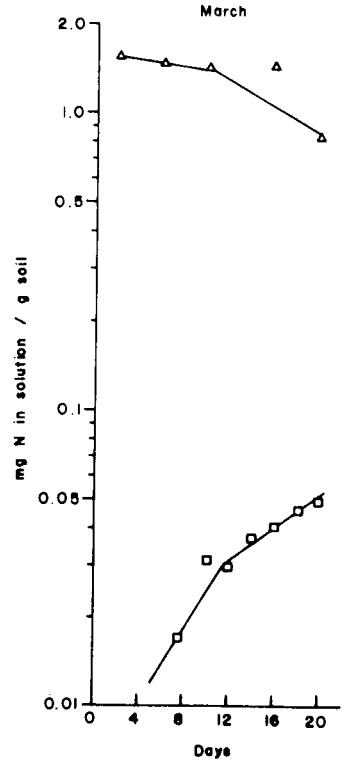
This experiment was carried out to find what minimum moisture level is necessary to significantly stimulate microbial activity in desert soils. Raw data on the findings are given in Table 12. The analysis of variance for respiration, dehydrogenase activity, and ATP concentration tested for ten soils and six moisture levels combined is given in Table 13. There was no significant difference in respiration between moisture levels nor soils. Mean and LSD values for dehydrogenase activity and ATP concentration tested for adjusted moisture levels are given in Table 14. Dehydrogenase activity was not significantly increased when soils were adjusted to -3, -14, and -23 bars, but was

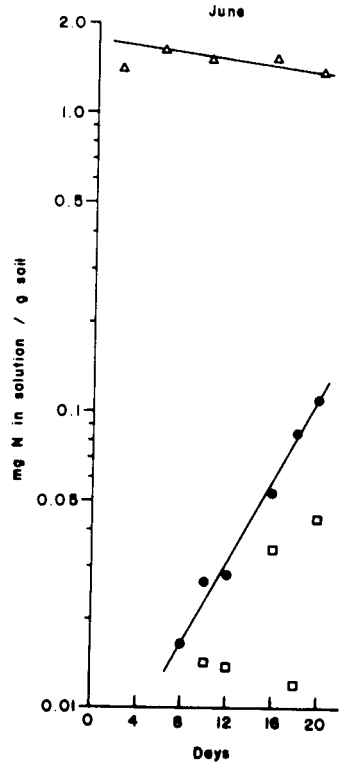
Figure 11. Date comparison of nitrification potential in Silverbell soils, average of duplicate samples.

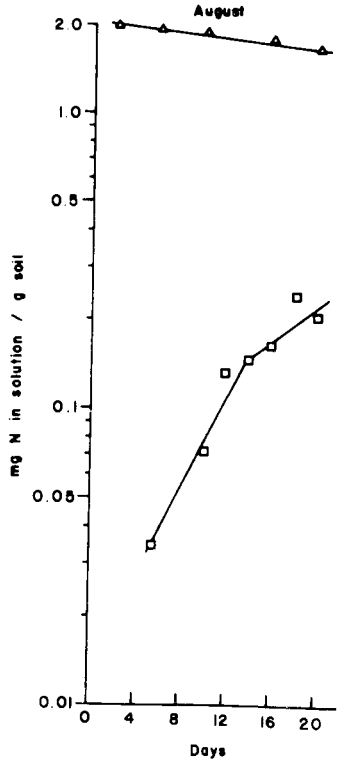
Δ - NH_4^+-N

● - NO_2^--N

□ - NO_3^--N


March
2.0
1.0
0.5
0.1
0.05
0.01
mg N in solution / g soil
0
4
8
12
16
20
Days


June
2.0
1.0
0.5
0.1
0.05
0.01
mg N in solution / g soil
0
4
8
12
16
20
Days


August
2.0
1.0
0.5
0.1
0.05
0.01
mg N in solution / g soil
0
4
8
12
16
20
Days

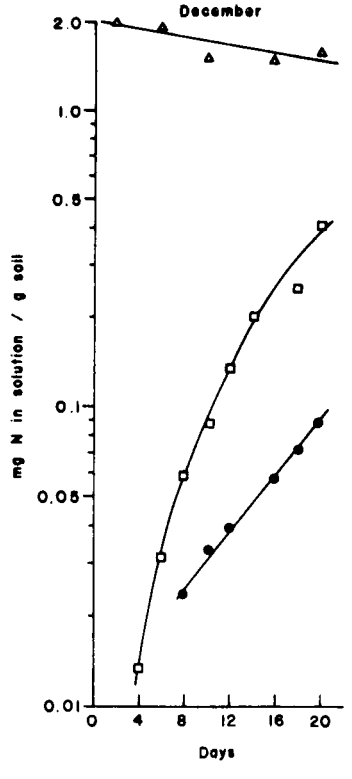
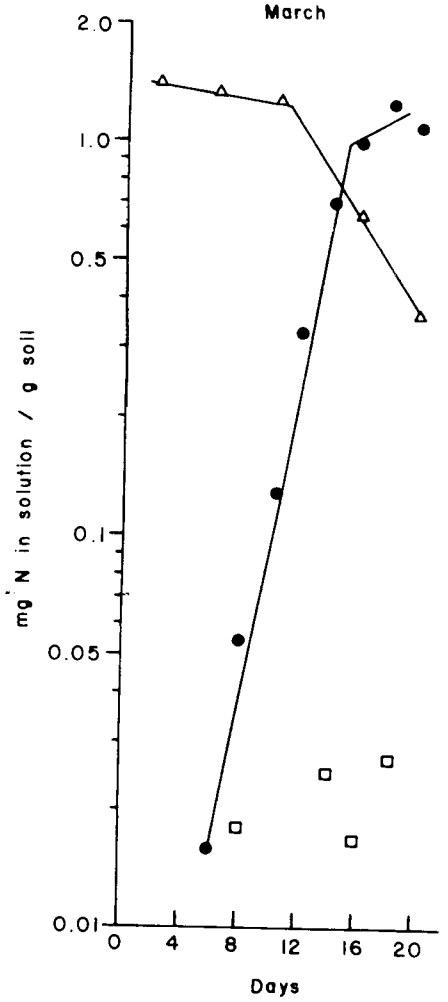

December
2.0
1.0
0.5
0.1
0.05
0.01
mg N in solution / g soil
0
4
8
12
16
20
Days

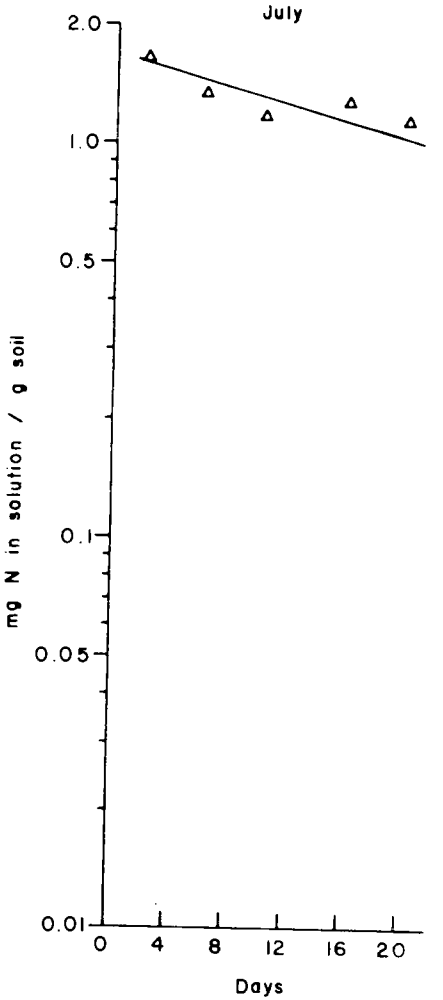
Figure 12. Date comparison of nitrification potential in Rock Valley soils, average of duplicate samples.

Δ - NH_4^+-N

● - NO_2^--N

□ - NO_3^--N


March
2.0
1.0
0.5
0.1
0.05
0.01
mg N in solution / g soil
0
4
8
12
16
20
Days


July
2.0
1.0
0.5
0.1
0.05
0.01
mg N in solution / g soil
0
4
8
12
16
20
Days

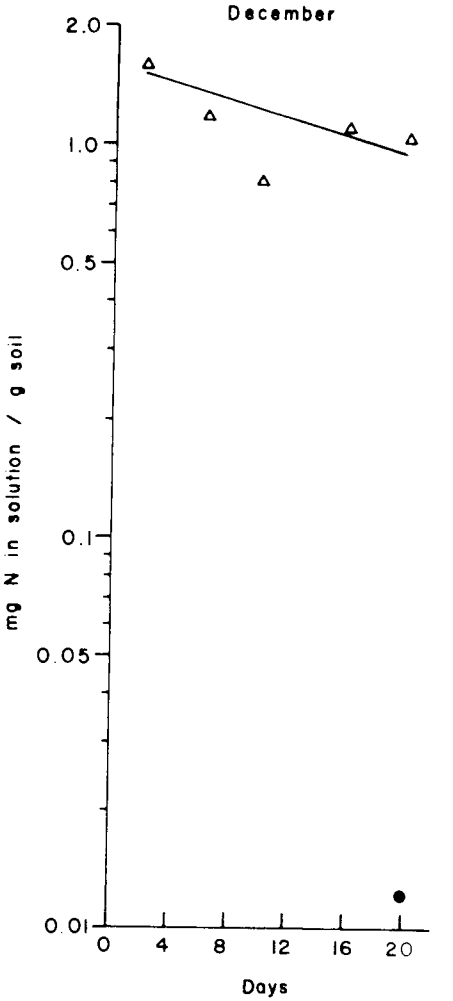
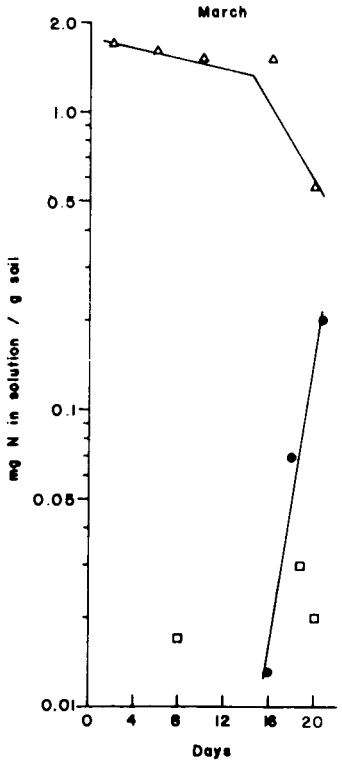

December
2.0
1.0
0.5
0.1
0.05
0.01
mg N in solution / g soil
0
4
8
12
16
20
Days

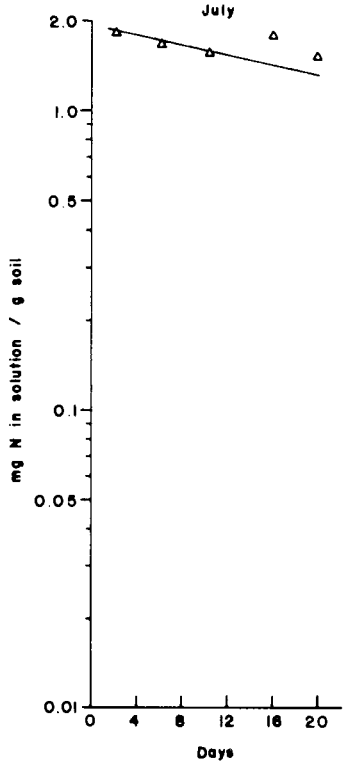
Figure 13. Date comparison of nitrification potential in Pine Valley soils, average of duplicate samples.

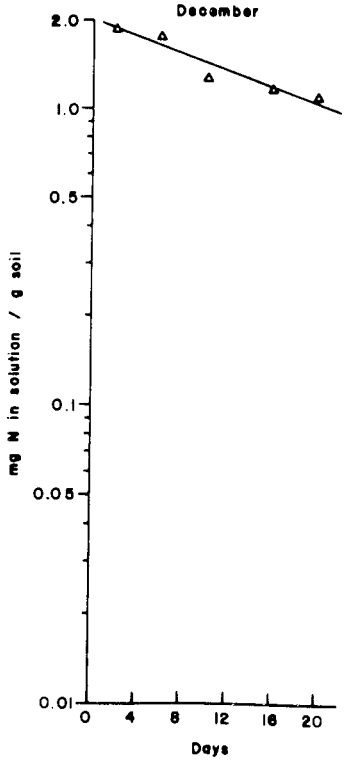
Δ - NH_4^+-N

● - NO_2^--N

□ - NO_3^--N


March
2.0
1.0
0.5
0.1
0.05
0.01
mg N in solution / g soil
0
4
8
12
16
20
Days


July
2.0
1.0
0.5
0.1
0.05
0.01
mg N in solution / g soil
0
4
8
12
16
20
Days


December
2.0
1.0
0.5
0.1
0.05
0.01
mg N in solution / g soil
0
4
8
12
16
20
Days

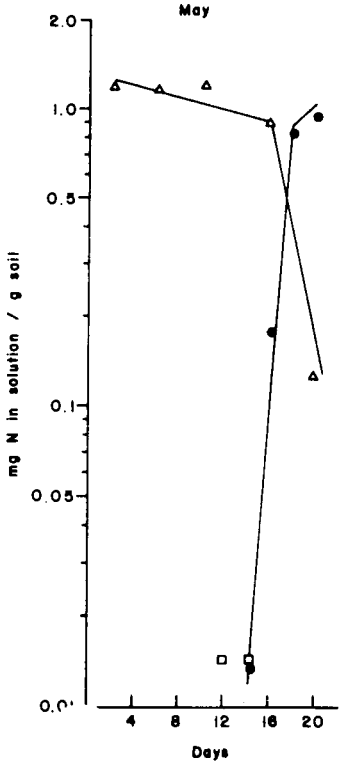

May
2.0
1.0
0.5
0.1
0.05
mg N in solution / g soil
4
8
12
16
20
Days

Figure 14. Date comparison of nitrification potential in Curlew soils, stations 5, 6, and 7 averaged.

Δ - NH_4^+-N

● - NO_2^--N

□ - NO_3^--N

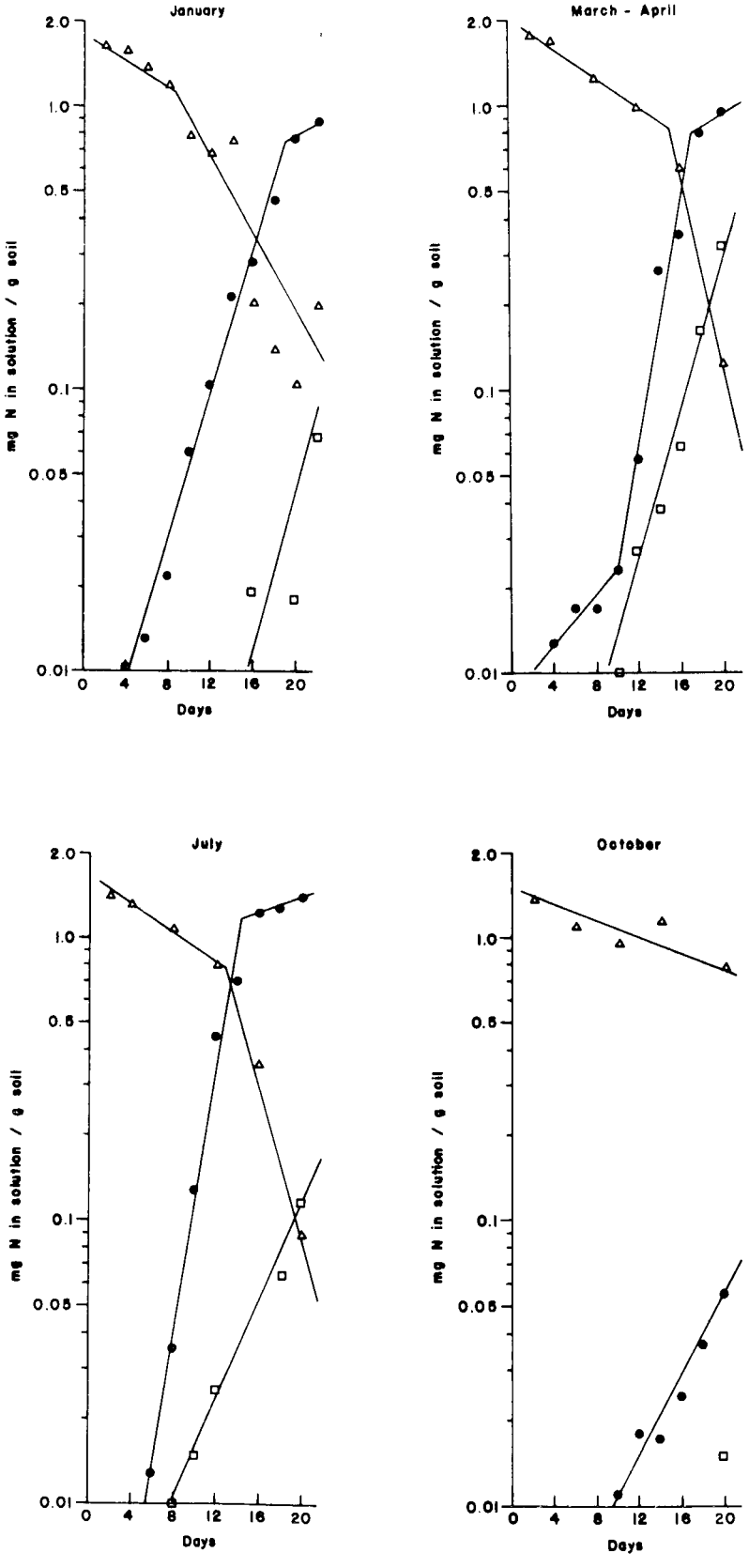

January
March - April
July
October
mg N in solution / g soil
2.0
1.0
0.5
0.1
0.05
0.01
0
4
8
12
16
20
Days

Table 12. Adjusted moisture experiment--respiration (Resp.)*, dehydrogenase activity (Dehydro)*, ATP concentration (ATP)*, and water potential (- bars) in ten soils at original moisture and five adjusted moisture levels

Sample	Original Moisture				Field Capacity				2/3 Field Capacity			
	Resp.	Dehydro	ATP	Bars	Resp.	Dehydro	ATP	Bars	Resp.	Dehydro	ATP	Bars
P	22.3	.182	.0096	<-100	31.0	.508	.0319	-0.3	36.7	.362	.0303	-1.5
B-1	4.1	.054	.0091	<-100	3.8	.125	.0260	-0.3	8.7	.115	.0212	-2.0
B-2	4.3	.038	.0077	<-100	2.5	.150	.0248	-0.3	21.0	.246	.0169	-1.8
B-3	2.4	.044	.0095	<-100	3.6	.226	.0371	-0.3	19.6	.277	.0188	-3.2
S	2.9	.077	.0084	<-100	8.5	.458	.0639	-0.3	15.3	.403	.0194	-2.0
RV	8.8	.049	.0077	<-100	6.0	.353	.0198	-0.3	9.6	.438	.0271	-2.0
PV	9.8	.586	.0069	<-100	4.4	.473	.0344	-0.3	13.0	.464	--	-1.0
C 5	14.4	.523	.0090	<-100	9.3	.446	.1049	-0.3	14.2	.518	.0695	-1.0
C 6	17.3	.892	.0064	<-100	19.1	1.116	.0875	-0.3	30.6	.621	.0938	-1.0
C 7	19.9	.716	.0134	<-100	15.2	1.135	0.752	-0.3	17.2	.883	.0654	-3.0

* Respiration units = μmoles CO_2 evolved/g/min
Dehydrogenase units = mg formazan formed/g
ATP units = μg/g

Table 12 Continued

Sample	1/2 Field Capacity				Air Dried				1/6 Field Capacity			
	Resp.	Dehydro	ATP	Bars	Resp.	Dehydro	ATP	Bars	Resp.	Dehydro	ATP	Bars
P	26.6	.498	.0429	4.3	19.0	.551	.0548	17.1	22.6	.667	.1301	21.0
B-1	2.4	.084	.0578	4.3	10.7	.130	.1058	23.0	3.8	.089	.1656	24.3
B-2	5.4	.099	.0332	4.0	8.2	.129	.0668	8.7	7.0	.114	.0483	28.2
B-3	7.6	.135	.1324	3.8	8.9	.130	.0923	13.5	8.6	.104	.1566	21.0
S	6.2	.272	.1972	3.5	6.1	.206	.0237	9.8	8.7	.231	.0971	21.9
RV	8.5	.185	.1039	2.3	5.1	.191	.1113	11.3	6.7	.140	.0826	24.1
PV	10.2	.269	.0777	1.5	8.8	.228	.0941	9.3	8.4	.232	.1224	25.0
C 5	14.2	.354	.1779	2.1	12.0	.620	.1550	14.1	9.0	.564	.1454	25.6
C 6	19.9	.944	.2433	2.1	15.3	1.004	.2697	20.8	15.3	1.044	.2124	23.1
C 7	25.6	.548	.0334	3.0	14.9	.506	.0341	16.7	21.2	.748	.1912	20.2

Table 13. Analysis of variance for respiration, dehydrogenase activity, and ATP concentration tested for ten soils and six moisture levels combined in Adjusted Moisture Level Experiment

Source of Variation	df	Expected Mean Square and Significance		
		Respiration (μmoles CO_2/g/min)	Dehydrogenase (mg formazan/g)	ATP μg/g
Soils (S)	9	4890.9	.931*	.014*
Moisture Level (M)	5	5988.9	.090*	.048*
S x M Interaction†	45	5437.9	.033	.003
Sampling	120	5518.8	.007	.001
Total	179	5480.0	.090	.005

* Alpha = .10

† S x M = error

Table 14. Mean and LSD values for dehydrogenase activity and ATP concentration tested at five moisture levels in Adjusted Moisture Level Experiment

Moisture	Dehydrogenase (mg formazan/s)	ATP (µg/g)
- 100 bars (original moisture)	0.3162	0.0085
-0.3 bar (field capacity)	0.4988	0.0499
-2.0 bars (2/3 field capacity)	0.4365	0.0391
-3.0 bars (1/2 field capacity)	0.3386	0.1126
-14 bars (1/6 field capacity)	0.3708	0.1023
-23 bars (air dried)	0.3932	0.1347

$LSD_{0.10}$: Dehydrogenase - 0.1158
ATP - 0.0349

significantly increased at -0.3 bars and -2 bars. On the other hand, ATP concentration was not significantly increased at -0.3 cars, -2 bars, and -3 bars, but was increased at -14 and -23 bars.

Mean and LSD values for dehydrogenase activity and ATP concentration in ten different soils are given in Table 15. Curlew 6 and 7 soils had highest dehydrogenase activity and Curlew 5 and 6 had highest ATP concentration.

Correlation coefficients between dehydrogenase activity, respiration and ATP are given in Table 16. Correlation between activities are similar at -0.3 bars and -14 bars. Dehydrogenase and ATP are negatively correlated at <-100 bars. Negative correlations also existed between dehydrogenase and respiration and between respiration and ATP at -3.0 bars.

Drying Experiment

This experiment was conducted to demonstrate the effect of drying on microbial activity in desert soils. Raw data on the findings are given in Table 17. Table 18 gives the analysis of variance for respiration, dehydrogenase activity, and ATP concentration tested for ten soils and seven drying intervals combined. There was no significant difference between drying intervals in dehydrogenase activity. Mean and LSD values for respiration and ATP concentration tested in seven drying intervals and ten soils combined are given in Table 19. Respiration is lowest in soil after 192 hours drying at $22^{o}C$ but with further drying at higher temperatures respiration increases.

Table 15. Mean and LSD values for dehydrogenase activity and ATP concentration in ten soils tested in the Adjusted Moisture Level Experiment

Sampling Station	Dehydrogenase (mg formazan/g)	ATP (μg/g)
P	0.461	0.0499
B-1	0.106	0.0647
B-2	0.129	0.0319
B-3	0.152	0.0739
S	0.275	0.0682
RV	0.226	0.0616
PV	0.375	0.0624
C 5	0.504	0.1115
C 6	0.937	0.1524
C 7	0.758	0.0687

$LSD_{0.10}$: Dehydrogenase = 0.224
ATP = 0.0529

Table 16. Correlation between dehydrogenase activity, respiration, and ATP in Adjusted Moisture Level Experiment

Moisture level/Activities	$r = \frac{\Sigma(x - \bar{x})(y - \bar{y})}{\sqrt{\Sigma(x - \bar{x})^2 \Sigma(y - \bar{y})^2}}$
Original Moisture (ave. bars = <-100)	
Dehydrogenase - Respiration	.65
Respiration - ATP	.19
Dehydrogenase - ATP	-.37
Field Capacity (ave. bars = -0.3)	
Dehydrogenase - Respiration	.58
Respiration - ATP	.24
Dehydrogenase - ATP	.63
2/3 Field Capacity (ave. bars = -2.0)	
Dehydrogenase - Respiration	.11
Respiration - ATP	.33
Dehydrogenase - ATP	.63
1/2 Field Capacity (ave. bars = -3.0)	
Dehydrogenase - Respiration	-.20
Respiration - ATP	-.62
Dehydrogenase - ATP	.37
Air Dried (ave. bars = -23)	
Dehydrogenase - Respiration	.73
Respiration -ATP	.33
Dehydrogenase - ATP	.59
1/6 Field Capacity (ave. bars = -14)	
Dehydrogenase - Respiration	.59
Respiration - ATP	.17
Dehydrogenase - ATP	.63

Table 17. Respiration (Resp.)*, dehydrogenase activity (Dehydro)*, ATP concentration (ATP)*, and water potential (- bars) in ten soils at different drying intervals during drying experiment

Sample	Original Moisture				Wetted				Air Dried 24 hrs at 22°C				Air Dried 96 hrs at 22°C			
	Resp.	Dehydro	ATP	Bars	Resp.	Dehydro	ATP	Bars	Resp.	Dehydro	ATP	Bars	Resp.	Dehydro	ATP	Bars
P	37.6	.110	.0114	<-100	29.7	.113	.0739	-10	18.8	.118	.0162	<-100	16.0	.081	.0159	<-300
B-1	9.2	.017	.0287	<-100	6.5	.021	.0694	- 6	3.6	.019	.0368	<-100	8.1	.014	.0283	<-300
B-2	9.5	.027	.0160	<-100	11.0	.029	.0842	- 5	6.5	.022	.0184	<-100	9.1	.022	.0187	<-300
B-3	7.5	.073	.0188	<-100	5.4	.012	.1136	- 4	7.2	.008	.0130	<-100	7.2	.009	.0182	<-300
S	7.6	.054	.0196	<-100	11.7	.059	.2180	- 4	5.6	.051	.0267	<-100	7.9	.042	.0385	<-300
RV	11.0	.029	.0186	<-100	8.9	.028	.0731	- 4	9.0	.027	.0192	<-100	11.9	.014	.0147	<-300
PV	20.6	.016	.0340	- 5	9.2	.018	.0549	- 6	11.2	.016	.0048	<-100	10.8	.012	.0069	<-300
C 5	31.9	.079	.0639	- 17	17.7	.047	.1398	- 6	15.5	.057	.0336	<-100	11.1	.053	.0177	<-300
C 6	28.5	.048	.1054	- 19	17.5	.040	.1874	- 4	15.1	.031	.0372	<-100	17.1	.068	.0217	<-300
C 7	24.9	.106	.0690	- 48	22.0	.172	.2141	- 5	13.3	.158	.0317	<-100	9.4	.134	.0214	<-300

* Respiration units = μmoles CO_2 evolved/g/min
Dehydrogenase units = mg formazan formed/g
ATP units = μg/g

Table 17. Continued

Sample	Air Dried 192 hrs at 22°C				Air Dried 192 hrs + 24 hrs at 30°C				Air Dried 192 hrs at 22°C + 24 hrs at 38°C + 24 hrs at 37°C			
	Resp.	Dehydro	ATP	Bars	Resp.	Dehydro	ATP	Bars	Resp.	Dehydro	ATP	Bars
P	10.0	.105	.0275	<-300	19.8	.110	.0250	<-300	11.0	.095	.0263	<-300
B-1	6.1	.024	.0410	<-300	7.4	.017	.0478	<-300	8.8	.027	.0415	<-300
B-2	6.5	.036	.0226	<-300	10.1	.020	.0280	<-300	11.0	.028	.0190	<-300
B-3	6.5	.011	.0332	<-300	8.7	.009	.0383	<-300	9.2	.016	.0343	<-300
S	11.7	.066	.0308	<-300	10.3	.058	.0680	<-300	14.6	.074	.0479	<-300
RV	6.6	.022	.0218	<-300	13.5	.023	.0286	<-300	13.2	.022	.0231	<-300
PV	11.0	.014	.0101	<-300	11.2	.011	.0355	<-300	12.5	.043	.0188	<-300
C 5	9.8	.042	.0266	<-300	12.7	.079	.0512	<-300	15.5	.062	.0442	<-300
C 6	5.9	.023	.0251	<-300	11.7	.094	.0295	<-300	16.1	.088	.0290	<-300
C 7	5.5	.118	.0237	<-300	10.3	.161	.0298	<-300	14.8	.140	.0535	<-300

Table 18. Analysis of variance for respiration, dehydrogenase activity, and ATP concentration tested for ten soils and seven drying intervals combined in Drying Experiment.

Source of Variation	df	Expected Mean Square and Significance		
		Respiration (μmoles CO_2/g/min)	Dehydrogenase (mg formazan/g)	ATP (μg/g)
Soils (S)	9	263.872*	.0205*	.0037*
Drying Intervals (D)	6	232.400*	.0016	.0264*
S x D†	54	38.446	.0008	.0013
Sampling	70	5.616	.0006	.0002
Total	139			

*Significant at Alpha = 0.10

†S x D = error

Table 19. Mean and LSD values for respiration and ATP concentration in seven drying intervals tested in Drying Experiment

Moisture Levels	Respiration (μmoles CO_2/g/min)	ATP (μg/g)
Original moisture	18.80	0.0385
Wetted soil	13.94	0.1228
Soil after 24 hrs drying	10.54	0.0226
Soil after 96 hrs drying	10.88	0.0173
Soil after 192 hrs drying	7.93	0.2623
Soil after 192 hrs drying plus 24 hrs at 30 C	11.565	0.0354
Soil after 24 hrs at 30 C plus 24 hrs at 37 C	12.65	0.0381
$LSD_{0.10}$:	Respiration = 3.810	
	ATP = 0.0221	

There was no abiotic CO_2 evolution measured in soils treated with propylene oxide at intervals of drying at room temperature. However, 8 percent abiotic CO_2 was measured after drying at 30°C. No abiotic CO_2 evolution was measured in soil after drying at 37°C but abiotic CO_2 evolution of lyophilized soil was 6 percent of the total CO_2 evolved.

ATP concentration is highest after 192 hours drying at 22°C and with further drying at higher temperatures ATP decreases to approximately the same levels as in the original moisture. ATP concentration fluctuates erratically between drying intervals.

Adjusted Moisture Level Plus Organic Matter Experiment

This experiment was conducted to examine the effect of added organic matter on soils adjusted to different moisture levels and to compare the influence of added organic matter on soils with high and low organic carbon content.

Raw data for this experiment are given in Table 20. Table 21 gives the analysis of variance for respiration and dehydrogenase activity tested for four soils and five moisture levels combined. The four soils used were playa and Curlew 7 soils (relative high in organic carbon), and Bajada 1 and Rock Valley soils (relatively low in organic carbon). There was no significant difference in respiration in the four soils and five moisture levels combined but there was a significant difference in dehydrogenase activity between soils and moisture levels.

Table 20. Adjusted Moisture Levels Plus Organic Matter Experiment--respiration (Resp.)[†], dehydrogenase activity (Dehydro.), water potential (-bars) in glucose amended Playa, Bajada 1, Rock V alley, and Curlew 7 soils at original moisture and four adjusted moisture levels

	Playa			Bajada 1			Rock Valley			Curlew 7		
Moisture Levels	Resp.	Dehydro	Bars	Resp.	Dehydro	Bars	Resp.	Dehydro	Bars	Resp.	Dehydro	Bars
Original Moisture	11.2	.111	-300	4.4	.017	-300	3.9	.032	-300	0.4	.098	-300
1/2 Field Capacity	81.5	.136	3	21.1	.028	4	27.4	.071	4	67.1	.121	3
1/4 Field Capacity	141.4	.099	14	22.9	.028	17	21.5	.048	18	53.4	.112	16
1/6 Field Capacity	83.4	.102	-130	0.5	.014	-160	17.5	.032	-175	48.7	.092	-153
1/12 Field Capacity	31.4	.108	-275	3.7	.034	-280	5.8	.040	-265	10.4	.096	259

[†]Respiration units = μmoles CO_2 evolved/g/min
Dehydrogenase units = mg formazan formed/g

Table 21. Analysis of variance for respiration and dehydrogenase activity tested for four soils and five moisture levels combined in Adjusted Moisture Level Plus Organic Matter Experiment

Source of Variation	df	Expected Mean Square and Significance	
		Respiration	Dehydrogenase
Soils (S)	3	2956.516	.0187*
Moisture level (M)	4	47690.10	.0010*
S x M† Interaction	12	45018.05	.00014
Sampling	40	49797.21	.0008
Total	59	46300.59	.0016

*Significant at Alpha = 0.10

†S x M = error

Mean and LSD values of dehydrogenase activity for five moisture levels is given in Table 22. There was no significant difference in dehydrogenase activity when moisture was increased from lyophilized soil at <-300 bars to -270 and -154 bars even with addition of glucose, a readily utilizable organic matter source.

Soils with relatively high organic carbon content had higher dehydrogenase activity than those with lower organic carbon content (see Table 23).

Wetting-Drying Experiment

This experiment was conducted to demonstrate the effect on microbial activity in desert soils of wetting a dry soil, allowing it to air dry for several days, and then rewetting it.

Raw data on respiration, dehydrogenase activity, and ATP concentration at four moisture intervals in ten soils with added organic matter are given in Table 24.

Respiration increases an average of 20-fold in lyophilized soil which was wetted, whereas dehydrogenase only increased an average of 2.7-fold and ATP concentration increased a trace on the average. An air dry soil which was rewetted increased in respiration by 36-fold and dehydrogenase increased by 5-fold. ATP concentration decreased slightly.

Since the added organic matter was casein, both a carbon and a nitrogen source, it is possible to examine the ammonification in the soils as affected by wetting and drying. Table 25 gives the total ammonium in the soils after moistening, subsequent air drying, and

then remoistening the air-dry soil. Ammonification increases in soils in the air-dry state and even more when soils are rewetted.

Table 22. Mean and LSD values of dehydrogenase activity for five moisture levels tested in Adjusted Moisture Plus Organic Matter Experiment

Moisture Level	Dehydrogenase (mg formazan/g)
-3.5 bars (1/2 field capacity)	0.0894
-16 bars (1/4 field capacity)	0.0714
-154 bars (1/6 field capacity)	0.0603
-270 bars (1/12 field capacity)	0.0693
< -300 bars (Lyophilized - original moisture)	0.0644

$LSD_{0.10} = 0.0126$

Table 23. Mean and LSD values of dehydrogenase activity for four sampling stations tested in Adjusted Moisture Plus Organic Matter Experiment

Sampling Station	Dehydrogenase (mg formazan/g)
Playa	0.112
Bajada 1	0.0238
Rock Valley	0.0448
Curlew 7	0.1039

$LSD_{0.10} = 0.0125$

Table 24. Wetting-drying experiment--respiration (Resp.), dehydrogenase (Dehydro.), and ATP concentration for soils at different moisture intervals

Stations	Lyophilized Soil			Soil Moistened to Field Capacity			Air Dry Soil			Rewetted Soil		
	Resp. (µmoles/g/min)	Dehydro. (mg formazan/g)	ATP (µg/g)	Resp. (µmoles/g/min)	Dehydro. (mg formazan/g)	ATP (µg/g)	Resp. (µmoles/g min)	Dehydro. (mg formazan/g)	ATP (µg/g)	Resp. (µmoles/g min)	Dehydro. (mg formazan/g)	ATP (µg/g)
P	13.4	.063	.0195	143.8	.382	.0359	15.7	.049	.0213	185.2	.685	.0241
B-1	3.4	.015	.0145	82.8	.052	.0299	5.6	.012	.0231	140.3	.196	.0337
B-2	3.6	.015	.0122	72.2	.043	.0118	6.4	.025	.0130	135.9	.196	.0119
B-3	6.0	.025	.0187	72.0	.057	.0165	5.7	.029	.0193	146.6	.070	.0092
S	4.3	.029	.0151	121.9	.070	.0101	3.8	.034	.0268	169.9	.233	.0065
RV	5.0	.040	.0082	136.1	.091	.0053	5.3	.090	.0104	226.6	.247	.0029
PV	4.2	.085	.0156	106.2	.132	.0090	8.1	.092	.0073	192.4	.321	
C 5	3.7	.067	.0211	100.2	.230	.0278	8.9	.121	.0147	248.6	.431	.0037
C 6	5.2	.113	.0210	132.5	.181	.0293	8.9	.196	.0356	229.9	1.058	.0034
C 7	4.5	.148	.0155	117.7	.401	.0104	16.5	.225	.0118	207.3	1.117	.0049

Table 25. Wetting-drying experiment--total ammonium in soils at moistened, air-dry and remoistened intervals with 1% w/w casein[†]

Soil Sample	mg NH_4^+-N/g		
	Moistened	Air Dry	Remoistened
P	0.511	0.495	0.747
B-1	0.194	0.247	0.450
B-2	0.101	0.299	0.479
B-3	0.204	0.391	0.384
S	0.125	0.298	0.424
RV	0.144	0.310	0.467
PV	0.137	0.238	0.326
C 5	0.164	0.466	0.513
C 6	0.206	0.376	0.570
C 7	0.189	0.352	0.690
Average and S.D.	0.198±.115	0.347±.086	0.505±.131

[†]2.759 mgN/g added.

DISCUSSION

Soil Analysis at Different Collection Periods

Chemical analysis of soils, given in Table 3, indicates that Curlew and Playa (Jornada) soils have the highest organic matter content. The physical nature of the sites from which these soils were collected explains the higher carbon and nitrogen content. *Panicum obtusum* covers the playa bottom where Playa soils were collected. The amount of residue available for oganic matter production is increased by the density of vegetation. Also, Playa soils were found to have high heterotrophic nitrogen fixation potential (Skujins 1977). Heterotrophic nitrogen fixing organisms such as *Azobacter* and *Clostridium* have been isolated from the rhizosphere in desert soils and play an important role in nitrogen input (Elwan and Mahmoud 1950).

Lynn and Cameron (1973) have reported that algal lichen crusts cover approximately 70 percent of the desert soil surface in Curlew. The blue-green algal components of the soil cryptogramic crusts have been found to fix high amounts of nitrogen (Rychert and Skujins 1974, West and Skujins 1977) and add organic matter to the system (Mayland, McIntosh, and Fuller 1966).

The pH of the soils is slightly alkaline. This influences the types of organisms which can proliferate under conditions of both drought and alkalinity. Thorton (1953) has stated that alkaline

soils have little diversification in microbial flora, consisting of mostly Actinomycetes.

According to Brock (1966) bacterial numbers must be at least 10^6 per gram before it can be concluded that they are making any significant contribution to the ecosystem. Table 4 gives microbial counts. If Brock's criterion is used, only aerobic bacteria make a significant contribution to the soils. The use of skim milk as the protein substrate in the media used to culture proteolytic organisms limited the growth to colonies which could utilize casein. Other protein substrates were not used and consequently other types of proteolytic organisms were not enumerated. Not all organisms present in the soil were cultured on the plates since microorganisms vary greatly in their nutritional requirements, and consequently no single medium and set of growth conditions will permit the growth of all microorganisms present in a natural population.

Seasonal patterns of soil moisture were a source of variation for dehydrogenase, ATP concentration, proteolytic activity, and nitrification potential tested for four dates (Table 6). However, the seasonal pattern of soil moisture was not a source of variation for respiration, dehydrogenase, and proteolysis for ten soils and four dates combined. The following hypothesis is thus rejected: that microbial activity as measured by respiration, dehydrogenase activity, and ATP concentration would not be significantly different between desert soils during the wet season.

Respiration, dehydrogenase activity, and ATP concentration each index total microbial activity. However, results suggest that each

one represents only a portion of the microbial metabolism which can be measured. They do not respond proportionally to each other as expected because of their close relationship in the ultimate pathway of metabolism. Correlation analysis, reported in Table 11, indicates significant correlation between respiration and ATP and not between respiration and dehydrogenase activity, nor dehydrogenase and ATP. Dommergues (1973) states that a positive or negative correlation between variables does not necessarily imply a cause-effect relation. He also contends that the absence of correlations between activities such as CO_2 evolution and dehydrogenase activity of a soil system should not be surprising when different experimental conditions are used to obtain results for each activity.

Thayer (1974) found no correlation between moisture and number of viable bacteria. Environmental conditions such as moisture are less apt to cause significant changes in total activity since several types of organisms contribute to the activity measured and each group responds differently. For example, Casida, Klein, and Santoro (1964) found that numbers of soil fungi and actinomycetes did not increase with nutrient addition and with moistening and drying of the soil.

Respiration was not significantly different between soils collected during the wet season. One difficulty with using respiration to estimate "biological activity" is that it is an aerobic process and anaerobic conditions may exist frequently in soil crumbs because there is an uneven distribution of water and, consequently, a presence of anaerobic zones (Greenwood 1968). The lowest respiration was measured in soils with a sandy loam texture. Since the soils are

coarse textured they have greater water infiltration capacity and better drainage and, consequently, have less occurrence of anaerobic zones. The finer textured soils, on the other hand, have more anerobic zones occurring when water is added to them, with a consequent lowering of respiration rates. This results in no net difference in respiration among soils collected during the wet season.

Proteolytic activity in soils of different desert regions was not significantly different during wet seasons. Nitrification potential in different desert soils was significantly different during wet seasons. Therefore, the hypothesis that both proteolytic activity and nitrification potential in desert soils would be significantly different is rejected. On the other hand, proteolytic activity was significantly higher in soils collected during the wet season although there were no significant differences between soils of different sampling stations. Proteolytic activity has been correlated with moisture content (Skujins 1967). Pieper et al. (1972) found decomposition to be closely associated with the amount of water being added to the soil.

Season of above-ground plant activity was associated with respiration rates for the various sampling stations. There were significant differences in respiration among soils collected in the season when above-ground plant activity took place. Proteolytic activity was found to be highest during the time that above-ground portions of higher plants were dormant. The following hypothesis is thus accepted: that parameters measuring decomposition would be highest during the seasons in which above-ground portions of higher plants were dormant.

This is confirmed in Comaner and Staffeldt's (1977) review of decomposition in deserts.

Proteolysis is the first step in the degradation of protein and has been found to vary during the season that higher plants showed above-ground growth. It follows then that hydrolysis of proteins would be potentially higher in a soil collected in a season when above-ground portions of higher plants are dormant and there is more dead plant material available for microbial degradation in the surface soil, the site where most microbial activity occurs (Charley and West 1977).

Differences in respiration among soils collected in seasons of plant dormancy could be due to different organic matter mineralization capacity of each soil. Lengkeek and Pengra (1973) found seasonal fluctuation in rate of mineralization as measured by CO_2 evolution to be related to temperature and soil water variations. The texture of soils in this study varies from a clay loam to silt and sandy loams. The organic carbon content varies proportionally with the amount of clay in the soil (see Table 3). Both clay and organic matter increase water holding capacity, consequently differences in CO_2 evoluation among soils may be due to differences in mineralization capacity, which in turn is influenced by soil water variations due to soil texture and organic matter content. Furthermore, Fuller (1975) states that the rate of decomposition in desert soils is controlled primarily by availability of substrate. Therefore, differences among soils in respiration would be more prominent during seasons where there is

more available substrate as ground litter such as seasons when above-ground portions of the plant are dormant.

Similarities were found among desert soils collected within the same region and from different regions. The analysis of variance (Table 7) gives means for eight soil parameters measured in ten different desert soils. There were no significant differences between Curlew stations 5, 6, and 7 for most parameters measured. Bajada stations 1, 2, and 3 are also similar to each other in parameters measured. Silvebell appears to be most similar to the Curlew soils. The cluster analysis shown in Figure 3 also suggests this similarity. Anomalously, the texture of Silverbell soils is sandy loam, whereas the texture of the Curlew soils is silt loam. Also, there is a geographical difference in the location of the desert sites where these soils were collected. Curlew sampling stations, as mentioned above, are located in the Great Basin Desert, the northernmost desert, and Silverbell is located in the Sonoran Desert, a southern desert extending into Mexico.

Principal components analysis indicated that variations between the desert soils tested were due mostly to respiration, dehydrogenase activity, and ATP concentration. Of the parameters measured, respiration, dehydrogenase activity, and ATP concentration explained 89 percent of the variability between desert soils. This may be because respiration, dehydrogenase activity, and ATP concentration in desert soils are dependent on organic substrate availibility. Organic substrate availability is dependent on environmental conditions and soil physical properties. Soils with different physical properties and weather

patterns will have different levels of substrate availability. Consequently, differences will be exhibited in respiration, dehydrogenase activity and ATP concentration.

The similarity between microbial activity of Silverbell and Curlew soils could be due to similar levels of available substrate. Although these deserts are from geographically distinct regions, similar precipitation patterns prevail and similarities in microbial activity could be due to similar moisture patterns which in turn affect substrate availability. Both deserts receive high amounts of precipitation during winter months (December to February). Also, there is only a 0.81 cm difference in precipitation between Silverbell and Curlew sites for months in which soils were collected.

Similarities in microbial activity among Bajada 1, 2, and 3 soils and among Curlew 5, 6, and 7 soils are due to similar soil properties and similar moisture patterns occurring within the site.

Nitrification Potential

Nitrification potential activity was found to be significantly different among ten soils collected during the wet season. The nitrifying population in desert soils appears to be active in desert soils which have a higher moisture content. It was found that the nitrification potential was highest in Playa and Curlew soils. These soils are classified as clay loam and silt loams, respectively. They consequently have a higher water-holding capacity and would tend to have greater moisture throughout the year. The higher moisture content is more conducive to proliferation of nitrifying organisms.

Nitrification has been shown to be a function of pH and moisture (Morrill and Dawson 1962, Mahendrappa et al. 1966). Maximum nitrate production was found to occur at moisture tensions of -0.5 to -0.15 bar (Dubey 1968, Miller and Johnson 1964, Sabey 1969). Greaves and Jones (1941) found that ammonifying bacteria could survive long periods of dehydration but nitrite- and nitrate-producting bacteria did not. The results of this study, however, showed that greatest nitrification potential occurred during the dry seasons.

Dehydrogenase activity and proteolytic activity were highest in soils collected during the wet season, suggesting more decompositional activity during the wet seasons. However, ammonium substrate may be more available to nitrifyers following the wet periods, increasing the nitrifying population and the nitrification potential during the dry seasons.

Several soils exhibited nitrite accumulation (Playa, Figure 5; Curlew, Figure 12). This is anomalous since the turnover rate for nitrite oxidizers is faster than that of ammonium oxidizers. The classic nitrification curve shows little if any nitrite accumulation. Stojanovic and Alexander (1968) demonstrated that at soil pH greater than 7.0 free ammonium is injurious to *Nitrobacter* and it acts as an inhibitor. They also observed the accumulation of nitrite in soils having high pH values. Martin, Buehrer, and Caster (1942) obtained similar results. This may explain the nitrite accumulation in these nitrification potential experiments, since the pH of most of the soils tested was above 7.0.

On the other hand, Neal (1969) found substances present in root extracts of plants that increase or invade grassland soils to inhibit nitrifying bacteria. West and Sjukins (1977) report that *Atriplex* and *Artemisia* litter inhibit nitrification and N-fixation. This may be an important mechanism among plants for conserving the low amount of available nitrogen present in desert soils. Rice (1974) suggested that inhibition of nitrification would also conserve energy the plant needs to reduce nitrate. Went (1970) states that allelopathic effects are more common in arid regions.

The nitrification experiments in this study show only potential nitrification activity. Since the soils were not enriched, the results are dependent on the existing nitrifying population and on the conditions during the experiment. If inhibition of nitrification is due to the allelopathic effect of the vegetation, it could be revealed in these potential experiments by reduced activity of the nitrite oxidizing population due to its underdevelopment.

Biochemical-Microbial Activities at Lowered Water Potentials

Respiration was not significantly different between moisture levels and dehydrogenase activity increases significantly when adjusted to -0.3 bars and -2.0 only. ATP concentration, however, increases significantly when adjusted to -14 and -23 bars. Therefore the hypothesis that respiration, dehydrogenase activity and ATP concentration increase significantly in desert soils moistened to less than -2 bars is rejected. The hypothesis can be accepted for ATP concentration alone, but rejected for both respiration and dehydrogenase activity.

More ATP is generated from aerobic respiration (Stanier et al. 1976). The increase of ATP at lower moisture levels could be due to more aerobic respiration because of fewer anaerobic zones in the soil pores. Water barriers to oxygen movement become limiting for bacterial respiration (Clark 1967). On the other hand, the higher dehydrogenase activity measured at the higher moisture levels could be due to the occurrence of processes such a denitrification or another anaerobic process which contributes to the oxidoreductase activity.

Respiration, dehydrogenase activity, and ATP concentration do not maintain the same correlation to each other at different adjusted moisture levels. These results suggest that microorganisms in desert soils have other metabolic pathways which they may use when environmental conditions change.

The adjusted moisture level plus organic matter experiments demonstrated that soils of higher organic matter content have higher microbial activity. Cameron (1961) found that the numbers of microorganisms in desert soils appear to be closely associated with the abundance of carbonaceous food material available for degradation and synthesis. The soils with a higher organic matter content may contain a larger zymogenous bacterial population than the soils with low organic matter content, and therefore could respond more markedly to added organic matter. Sorensen (1974) found that addition of decomposable organic material to a soil resulted in an increased decomposition of native soil organic matter as compared to the controls without addition. This is known as a "priming effect," the cause of which could be an abundant production of enzymes or a development of

special groups of microorganisms as a result of the addition of decomposable organic material (Sorensen 1974).

There was no significant decrease in dehydrogenase between drying intervals in the drying experiment. Respiration, on the other hand, increased with further drying at temperatures higher than room temperature. ATP concentration fluctuated between drying intervals too much to show any trend. The following hypothesis is thus rejected: that respiration, dehydrogenase activity, and ATP concentration decrease initially upon desiccation of soil but upon further desiccation do not significantly decrease. There was no significant decrease in dehydrogenase between drying intervals.

Waksman (1952) has stated that heating a soil seems to improve it as a medium for bacterial growth. Oien et al. (1974) found increased temperatures applied during drying temporarily stimulated the microbial population. This may explain the increased respiration upon temperature increase during the drying experiment.

There was no significant decrease in dehydrogenase activity during drying intervals. None of the activities measured in the drying experiment responded alike. The results of this experiment suggest that respiration, dehydrogenase activity, and ATP concentration each represent a different phase of microbial activity or different groups of microorganisms in desert soils since they each behave differently under different moisture conditions. Binet (1973) has stated that dryness could favor certain categories of microorganisms and reduce activity of other microorganisms. He adds that the activity of

different microorganisms does not decrease at the same rate as desiccation of the soil.

The wetting-drying experiment demonstrated that there is definitely an increase in activity after a soil has been dried and is rewetted. The results are similar to those described by Birch (1958). Ammonification increased in soils in the air dry state and even more when soils were rewetted. Ammonifying bacteria have been found to be resistant to desiccation (Greaves and Jones 1941). The results of wetting and drying a soil is known as the Birch Effect and is probably responsible for the major portion of organic matter decomposition and subsequent mineralization taking place in desert soils (Charley 1972).

The results of this study indicate that desert soil has a specialized microbial population. Microorganisms in desert soils are able to function the same as microorganisms from other environments but have evolved tolerances to extreme conditions. Metabolic pathways may have also changed in order to conserve energy which instead can be used for survival mechanisms. There is evidence for the increasing order of complexity of electron transport chains in bacteria which may relate to the evoluationary development of more efficient pathways for the conservation of energy (Haddock and Jones 1977).

Because of the moisture limitation, decomposition in surface desert soils is limited to short periods after rain or dew; however, as is shown in this study, activity can be considerable even under dry conditions.

CONCLUSIONS

Soils collected from four geographically separated deserts of the western United States (Great Basin, Sonoran, Chihuahuan, and Mojave) during different moisture seasons exhibited fluctuations in microbial activity as measured by respiration, dehydrogenase activity, ATP concentration, proteolytic activity and nitrification potential.

Increase in soil moisture as modified by precipitation, did not cause a significant difference in respiration or proteolysis between desert soils, however, an increase in moisture did cause a significant difference in nitrification potential in different desert soils. Therefore, moisture availability appears to be a major influencing factor regulating nitrification potential of desert soils.

Low nitrification potential of desert soils was found. Nitrite accumulation in perfusion experiments, but not in field, was noted. Proteolytic activity was highest in soils collected when above-ground portions of desert plants were dormant.

Respiration, dehydrogenase activity, and ATP concentration did not respond proportionally in desert soils adjusted to different moisture levels. These results sugggest that respiration, dehydrogenase activity, and ATP concentration each appear to represent a different phase of microbial metabolism in desert soils.

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APPENDIX

Table 26. NaCl standard calibration curve used to determine water potential at 25°C

Molality of NaCl[†]	Average[**] μ volt readings	Water Potential bars
0.05	3.5	-2.3
0.10	14.5	-4.6
0.20	18.5	-9.2
0.50	35.0	-22.8
0.70	44.0	-32.1
0.90	49.0	-41.6
1.00	56.0	-46.4
1.10	66.0	-51.3
1.30	70.0	-61.2
1.50	80.0	-71.3
1.70	96.0	-81.7
1.90	110.0	-92.4
2.00	120.0	-97.8

[†]Water potentials of NaCl solutions determined by Lang (1967).

[**]Average of triplicate readings.

Table 27. $LiCl_2$ standard calibration curve used to determine water potential at 25°C

Molality of $LiCl_2$ †	Average** µvolt reading	Water Potential bars
1.81	40.0	-100
3.10	73.0	-200
4.12	112.0	-300
5.00	123.0	-400
5.77	158.0	-500
6.49	180.0	-600
7.00	205.0	-700
7.73	230.0	-800
8.30	255.0	-900
8.85	280.0	-1000

†Water potentials of $LiCl_2$ solutions determined by Robinson and Stokes (1949).

**Average of triplicate readings.

Table 28. Nitrification potential station comparison (all collection dates averaged for each sample--standard error given)

Day Perfusion	Playa			Bajada 1			Bajada 2			Bajada 3			Silverbell		
	NH_4^+ µg/g	NO_2^- µg/g	NO_3^- µg/g	NH_4^+ µg/g	NO_2^- µg/g	NO_3^- µg/g	NH_4^+ µg/g	NO_2^- µg/g	NO_3^- µg/g	NH_4^+ µg/g	NO_2^- µg/g	NO_3^- µg/g	NH_4^+ µg/g	NO_2^- µg/g	NO_3^- µg/g
2	1.194 ±.05	0.005 ±.001	0.005 ±.002	1.749 ±.020	0.001 0	0.001 ±.001	1.721 ±.058	0.001 0	0.001 ±.001	1.743 ±.062	0.001 ±.001	0	1.821 ±.117	0.001 0	0.003 ±.001
4	--	0.026 ±.007	0.021 ±.005	--	0.001 0	0	--	0.001 ±.001	0.003 ±.001	--	0.001 0	0	--	0.001 0	0.008 ±.003
6	1.020 ±.08	0.082 ±.082	0.037 ±.011	1.637 ±.064	0.001 ±.001	0.001 ±.001	1.618 ±.093	0.002 ±.002	0.001 ±.001	1.663 ±.063	0.001 0	0	1.886 ±.107	0.004 0	0.020 ±.002
8	--	0.238 ±.050	0.103 ±.021	--	0.002 ±.001	0.002 ±.001	--	0.005 ±.004	0.001 ±.001	--	0.001 0	0.006 ±.002	--	0.012 ±.004	0.042 ±.014
10	0.888 ±.08	0.446 ±.135	0.147 ±.034	1.525 ±.083	0.003 ±.002	0.002 ±.001	1.362 ±.092	0.164 ±.013	0.004 ±.002	1.561 ±.058	0.001 0	0.005 ±.001	1.651 ±.069	0.018 ±.007	0.067 ±.019
12	--	0.645 ±.080	0.200 ±.040	--	0.005 ±.002	0.002 ±.001	--	0.044 ±.038	0.001 ±.002	--	0.003 ±.001	0.009 ±.003	--	0.019 ±.010	0.075 ±.022
14	--	0.860 ±.123	0.511 ±.136	--	0.005 ±.003	0.004 ±.001	--	0.108 ±.097	0	--	0.014 ±.009	0.011 ±.004	--	0	0.092 ±.036
16	0.404 ±.13	0.920 ±.088	0.424 ±.088	1.494 ±.065	0.015 ±.002	0.005 ±.001	1.103 ±.085	0.144 ±.066	0.002 ±.002	1.686 ±.117	0.021 ±.012	0.014 ±.003	1.551 ±.110	0.032 ±.017	0.141 ±.038
18	--	0.943 ±.145	0.518 ±.097	--	0.010 ±.005	0.004 ±.003	--	0.225 ±.085	0.003 ±.001	--	0.033 ±.018	0.020 ±.003	--	--	0.130 ±.043
20	0.168 ±.08	0.733 ±.136	0.608 ±.124	1.471 ±.207	0.028 ±.015	0.008 ±.003	0.861 ±.134	0.248 ±.108	0.003 ±.002	1.024 ±.187	0.045 ±.018	0.019 ±.004	1.333 ±.197	0.048 ±.025	0.154 ±.047

Table 29. Nitrification potential in playa soils collected in March, June, August, and December (standard error given)

Day	March			June			August			December		
	NH_4^+ µg/g	NO_2^- µg/g	NO_3^- µg/g	NH_4^+ µg/g	NO_2^- µg/g	NO_3^- µg/g	NH_4^+ µg/g	NO_2^- µg/g	NO_3^- µg/g	NH_4^+ µg/g	NO_2^- µg/g	NO_3^- µg/g
2	1.118 ±.064	0.009 ±.001	0.011 ±0	1.248 ±.092	0.006 ±.002	0.006 ±.006	1.087 ±.018	0.002 ±0	0.004 ±.004	1.323 ±.113	0.003 ±.001	0
4	--	0.036 ±.003	0.035 ±.002	--	0.052 ±.004	0.030 ±.011	--	0.009 ±.001	0.014 ±.003	--	0.009 ±.003	0.004 ±0
6	0.875 ±.023	0.147 ±.018	0.043 ±.003	0.876 ±.018	0.129 ±.052	0.076 ±.022	0.932 ±.055	0.015 ±.002	0.013 ±0	1.399 ±.001	0.039 ±.008	0.016 ±.003
8	--	0.377 ±.054	0.132 ±.049	--	0.354 ±.012	0.167 ±.020	--	0.083 ±.008	0.053 ±.007	--	0.138 ±.024	0.062 ±.012
10	0.669 ±0	0.688 ±.019	0.243 ±.015	0.745 ±.132	0.196 ±.136	0.221 ±.041	1.197 ±.019	0.155 ±.055	0.067 ±.002	0.942 ±.027	0.747 ±.438	0.056 ±.023
12	--	0.880 ±.119	0.227 ±.014	--	0.749 ±.057	0.329 ±.006	--	0.490 ±.187	0.103 ±.017	--	0.463 ±.041	0.091 ±.016
14	--	1.155 ±.110	0.482 ±.022	--	0.920 ±.079	0.890 ±.083	--	0.505 ±.135	0.161 ±.044	--	---	--
16	0.004 ±0	1.017 ±.110	0.647 ±.029	0.261 ±.204	1.064 ±.031	0.666 ±0	0.831 ±.146	0.776 ±.118	0.214 ±.023	0.520 ±.108	0.824 ±.361	0.169 ±.014
18	--	0.559 ±.101	0.802 ±.029	--	0.902 ±.035	0.736 ±.053	--	1.123 ±.201	0.285 ±.046	--	1.187 ±.543	0.250 ±.033
20	0.001 ±0	0.245 ±.233	0.810 ±.041	0.034 ±.007	0.784 ±.022	0.955 ±.272	0.147 ±.037	0.748 ±.017	0.452 ±.120	0.489 ±.086	1.157 ±.198	0.215 ±.055

Table 30. Nitrification potential in Bajada 1 soils collected in March, June, August, and December (standard error given)

Day	March			June			August			December		
	NH_4^+ µg/g	NO_2^- µg/g	NO_3^- µg/g	NH_4^+ µg/g	NO_2^- µg/g	NO_3^- µg/g	NH_4^+ µg/g	NO_2^- µg/g	NO_3^- µg/g	NH_4^+ µg/g	NO_2^- µg/g	NO_3^- µg/g
2	1.702 ±.013	0	0.005 ±.005	1.763 ±.021	0.001 ±0	0	1.717 ±.051	0.001 ±0	0.001 ±.001	1.814 ±.017	0	0
4	--	0	0	--	0.001 ±0		--	0.002 ±.001	0	--	0.001 ±0	0.001 ±.001
6	1.525 ±.038	0	0.005 ±.005	1.658 ±.017	0	0	1.467 ±.055	0.003 ±.002	0.001 ±.001	1.899 ±0	0.001 ±0	0.001 ±.001
8	--	0.001 ±.001	0.002 ±.002	--	0	0.001 ±.001	--	0.004 ±.004	0.004 ±.004	--	0.003 ±.001	0
10	1.777 ±.072	0.001 ±.001	0	1.659 ±.051	0	0	1.123 ±.064	0.007 ±.007	0.006 ±.006	1.444 ±.056	0.005 ±.001	0.002 ±.002
12	--	0.002 ±.002	0.003 ±.003	--	0	0	--	0.005 ±.005	0.006 ±.006	--	0.011 ±.002	0.002 ±.002
14	--	0.007 ±.007	0.003 ±.003	--	0	0.007 ±.002	--	0.007 ±.007	0.004 ±0	--	--	--
16	1.357 ±.206	0.008 ±.008	0.004 ±.003	1.646 ±.047	0	0.005 ±.005	1.455 ±0	0.012 ±.012	0.008 ±.001	1.499 ±.017	0.040 ±.019	0.002 ±.002
18	--	0.013 ±.013	0	--	0	0	--	0.011 ±.011	0.016 ±.033	--	0.018 ±.012	0.002 ±.002
20	1.298 ±.214	0.020 ±.020	0	1.296 ±.034	0.001 ±.001	0.005 ±0	1.3955 ±.948	0.013 ±.013	0.017 ±.003	1.895 ±.090	0.080 ±.042	0.012 ±.003

Table 31. Nitrification potential in Bajada 2 soils collected in March, June, August, and December (standard error given)

Day Perfusion	March			June			August			December		
	NH_4^+ µg/g	NO_2^- µg/g	NO_3^- µg/g	NH_4^+ µg/g	NO_2^- µg/g	NO_3^- µg/g	NH_4^+ µg/g	NO_2^- µg/g	NO_3^- µg/g	NH_4^+ µg/g	NO_2^- µg/g	NO_3^- µg/g
2	1.714 ±.034	0.001 ±.001	0.004 ±0	1.694 ±.088	0.002 ±.002	0.001 ±.001	1.576 ±.123	0	0.001 ±.001	1.902 ±.129	0	0
4	--	0.001 ±0	0.007 ±.003	--	0.003 ±.003	0.001 ±.001	--	0	0	--	0.001 ±0	0.004 ±.004
6	1.378 ±.076	0.001 ±.001	0.004 ±0	1.673 ±.210	0.007 ±.007	0	1.543 ±.216	0	0	1.829 ±.202	0.002 ±.001	0
8	--	0.001 ±.001	0.006 ±.003	--	0.017 ±.017	0	--	0.001 ±.001	0	--	0.004 ±.001	0
10	1.080 ±.240	0.002 ±.002	0.010 ±.003	1.480 ±.126	0.055 ±.055	0	1.530 ±.144	0.001 ±0	0	1.360 ±.146	0.008 ±.002	0.007 ±.006
12	--	0.005 ±.005	0	--	0.153 ±.153	0	--	0.001 ±0	0	--	0.018 ±.002	0.004 ±.003
14	--	0.027 ±.024	0	--	0.296 ±.294	0	--	0.002 ±0	0	--	--	--
16	1.076 ±.009	0.105 ±.093	0	0.892 ±.017	0.271 ±.260	0.007 ±.006	1.314 ±.300	0.002 ±0	0	1.132 ±.142	0.120 ±.061	0
18	--	0.281 ±.251	0	--	0.304 ±.269	0.008 ±.003	--	0.002 ±0	0.003 ±.003	--	0.313 ±.033	0
20	0.685 ±.609	0.031 ±.013	0	0.690 ±.009	0.381 ±.283	0.011 ±.001	1.044 ±.005	0.003 ±.001	0	1.024 ±.112	0.579 ±.119	0.001 ±0

Table 32. Nitrification potential in Bajada 3 soils collected in March, June, August, and December (standard error given)

Day Perfusion	March			June			August			December		
	NH_4^+ µg/g	NO_2^- µg/g	NO_3^- µg/g	NH_4^+ µg/g	NO_2^- µg/g	NO_3^- µg/g	NH_4^+ µg/g	NO_2^- µg/g	NO_3^- µg/g	NH_4^+ µg/g	NO_2^- µg/g	NO_3^- µg/g
2	1.593 ±.097	0	0	1.854 ±.072	0	0	1.610 ±.089	0.004 ±.003	0	1.915 ±.055	0	0
4	--	0.001 ±0	0	--	0.001 ±0	0	--	0.002 ±.001	0.001 ±.001	--	0.001 ±0	0
6	1.517 ±.021	0.001 ±0	0	1.585 ±.088	0.001 ±.001	0	1.665 ±.144	0.002 ±.001	0	1.885 ±.085	0.001 ±0	0
8	--	0.001 ±.001	0.004 ±0	--	0.001 ±.001	0.004 ±0	--	0.002 ±.001	0.010 ±.007	--	0.001 ±0	0.007 ±.003
10	1.394 ±0	0.001 ±0	0.003 ±0	1.552 ±.089	0.002 ±.001	0.006 ±.003	1.747 ±.072	0.001 ±0	0.007 ±.002	1.563 ±.145	0.001 ±0	0.007 ±.003
12	--	0.001 ±.001	0.005 ±.005	--	0.005 ±.001	0.017 ±.008	--	0.004 ±.004	0.011 ±.006	--	0.001 ±.001	0.004 ±.004
14	--	0.002 ±.002	0.020 ±.003	--	0.038 ±.015	0.005 ±0	--	0.002 ±.002	0.008 ±.008	--	0	0
16	1.394 ±.017	0.002 ±.002	0.023 ±.006	1.552 ±.013	0.078 ±0010	0.020 ±.005	2.028 ±.194	0	0.011 ±.006	1.367 ±.246	0.006 ±.002	0.004 +0
18	--	0.002 ±0	0.023 ±.011	--	0.116 ±.018	0.021 ±0	--	0	0.025 ±.006	--	0.016 ±.006	0.012 ±.003
20	0.267 ±.199	0.028 ±.028	0.013 ±.013	1.182 ±.030	0.121 ±.006	0.023 ±.002	1.154 ±.250	0	0.020 ±.011	1.495 ±.200	0.031 ±.009	0.020 ±.006

Table 33. Nitrification potential in Silverbell soils collected in March, June, August, and December (standard error given)

Day Perfusion	March			June			August			December		
	NH_4^+ µg/g	NO_2^- µg/g	NO_3^- µg/g	NH_4^+ µg/g	NO_2^- µg/g	NO_3^- µg/g	NH_4^+ µg/g	NO_2^- µg/g	NO_3^- µg/g	NH_4^+ µg/g	NO_2^- µg/g	NO_3^- µg/g
2	1.641 ±0	0.001 ±0	0.004 ±.003	1.562 ±.386	0	0.005 ±.005	2.066 ±.057	0.001 ±0	0.003 ±.003	2.015 +.187	0	0.001 ±.001
4	--	0	0.005 ±.005	--	0.001 ±0	0.002 ±.002	--	0.003 ±.001	0.008 ±.008	--	0.001 +0	0.015 ±.004
6	1.641 ±0	0	0	1.701 ±.214	0.001 ±0	0.005 ±.005	2.201 ±.201	0.007 ±.003	0.038 ±.011	2.001 ±.173	0.007 ±.001	0.036 ±.009
8	--	0	0.015 ±.010	--	0.017 ±.002	0	--	0.008 ±.005	0.079 ±.014	--	0.025 ±.005	0.073 ±.014
10	1.590 ±.009	0	0.023 ±.003	1.546 ±.017	0.031 ±.031	0.014 ±.004	1.957 ±.018	0.006 ±.005	0.132 ±.017	1.514 ±.076	0.037 ±.023	0.098 ±.009
12	--	0	0.021 ±0	--	0.031 ±.001	0.013 ±.003	--	0.001 ±.001	0.137 ±.003	--	0.043 ±.038	0.131 ±.020
14	--	0	0.030 ±.003	--	0	0	--	0.001 ±.001	0.153 ±.005	--	--	--
16	1.414 ±.065	0	0.038 ±.003	1.600 ±.424	0.065 ±.007	0.029 ±0	1.816 ±0	0.001 ±.001	0.216 ±.003	1.509 ±.098	0.062 ±.060	0.227 ±.022
18	--	0	0.042 ±.004	--	0.095 ±.017	0.013 ±.009	--	0.001 ±.001	0.186 ±.028	--	0.072 ±.070	0.282 ±.050
20	0.546 ±.031	0	0.051 ±.008	1.407 ±.231	0.101 ±.002	0.034 ±.008	1.511 ±.211	0.001 ±.001	0.196 ±.044	1.368 ±.226	0.091 ±.089	0.336 ±.011

Table 34. Nitrification potentail in Rock Valley soils collected in March, July, and December (standard error given)

Day Perfusion	March			July			December		
	NH_4^+ µg/g	NO_2^- µg/g	NO_3^- µg/g	NH_4^+ µg/g	NO_2^- µg/g	NO_3^- µg/g	NH_4^+ µg/g	NO_2^- µg/g	NO_3^- µg/g
2	1.512 ±0	0.002 ±.001	0	1.797 ±.017	0.002 ±.001	0	1.616 ±.073	0.003 ±.002	0
4	--	0.005 ±.003	0.001 ±.001	--	0.002 ±0	0	--	0.002 ±.001	0
6	1.400 ±.035	0.016 ±.013	0.006 ±.006	1.324 ±.034	0.002 ±.001	0	1.577 ±.034	0.002 ±0	0.001 ±0
8	--	0.055 ±.050	0.019 ±.015	--	0.002 ±.001	0	--	0.002 ±.001	0.003 ±.003
10	1.295 ±.156	0.129 ±.117	0.002 ±.002	1.164 ±.017	0.002 ±.001	0	0.797 ±.294	0.002 ±0	0
12	--	0.336 ±.290	0.009 ±.008	--	0.001 ±.001	0	--	0.002 ±.001	0
14	--	0.758 ±.634	0.022 ±.006	--	--	0	--	--	--
16	0.513 ±.435	0.912 ±.713	0.014 ±.003	1.413 ±.300	0.001 ±.001	0	1.040 ±.026	0.001 ±.001	0.003 ±.003
18	--	1.216 ±.826	0.023 ±.010	--	0.001 ±.001	0	--	0.004 ±.003	0.006 ±.006
20	0.287 ±.278	1.088 ±.459	0.008 ±0	1.063 ±.203	0	0	1.015 ±.111	0.013 ±.012	0.008 ±.008

Table 35. Nitrification potential in Pine Valley soil collected in March, July, December, and May (standard error given)

Day Perfusion	March			July			December			May		
	NH_4^+ µg/g	NO_2^- µg/g	NO_3^- µg/g	NH_4^+ µg/g	NO_2^- µg/g	NO_3^- µg/g	NH_4^+ µg/g	NO_2^- µg/g	NO_3^- µg/g	NH_4^+ µg/g	NO_2^- µg/g	NO_3^- µg/g
2	1.751 ±.041	0.001 ±0	0	1.863 ±0	0.001 ±0	0	1.919 ±.234	0.002 ±.001	0	1.255 ±0	0.002 ±.002	0.003 ±.003
4	--	0.001 ±0	0	--	0.001 ±0	0	--	0.003 ±0	0.001 ±.001	--	0	0
6	1.521 ±.041	0.002 ±0	0.001 ±.001	1.599 ±.091	0.001 ±0	0	1.613 ±.107	0.005 ±.001	0.003 ±.003	1.124 ±.131	0.004 ±.001	0.007 ±.004
8	--	0.002 ±0	0.017 ±.017	--	0.001 ±0	0	--	0.004 ±0	0	--	0.003 +0	--
10	1.420 ±.078	0.003 ±.001	0.005 ±.005	1.231 ±.052	0.001 ±.001	0	1.174 ±.034	0.003 ±0	0.007 ±.003	1.341 ±.128	0.001 ±0	0.005 +.005
12	--	0.004 ±.001	0	--	0.001 ±.001	0	--	0.004 ±.001	0.007 ±.003	--	0.002 ±0	0.015 ±.003
14	--	0.004 ±.002	0	--	0	0	--	--	--	--	0.015 ±.008	0.016 ±0
16	1.195 ±.019	0.013 ±.008	0.009 ±.006	1.837 ±.182	0.001 ±.001	0	1.085 ±.107	0.001 ±0	0	0.760 ±.132	0.185 ±.038	0.003 ±.003
18	--	0.069 ±.050	0.023 ±.005	--	0.001 ±.001	0	--	0.005 ±.003	0	--	0.678 ±.031	0.003 ±.003
20	0.427 ±.069	0.199 ±.149	0.017 ±.011	0.958 ±.343	0.002 ±.002	0	1.030 ±.094	0.004 ±.002	0.002 ±.002	0.123 ±.064	0.725 +.156	0

Table 36. Nitrification potential in January, March and April, July, and October Curlew 0-5 cm surface samples. Stations 5, 6, and 7 averaged (standard error given)

Day Perfusion	January			March-April			July			October		
	NH_4^+ µg/g	NO_2^- µg/g	NO_3^- µg/g	NH_4^+ µg/g	NO_2^- µg/g	NO_3^- µg/g	NH_4^+ µg/g	NO_2^- µg/g	NO_3^- µg/g	NH_4^+ µg/g	NO_2^- µg/g	NO_3^- µg/g
2	1.663 ±.163	0.002 ±.002	0	1.553 ±.099	0.431 ±.142	0.054 ±.035	1.350 ±.094	0.393 ±.189	0.037 ±0.25	1.569 ±.185	0.014 ±.008	0
4	1.628 ±.140	0.010 ±.001	0	1.495 ±.123	0.844 ±.269	0.120 ±.081	1.374 ±.003	0.998 ±.550	0.065 ±.045	--	0.008 ±0	0.001 ±.001
6	1.423 ±.220	0.013 ±.003	0	0.681 ±.171	0.660 ±.185	0.110 ±.069	0.502 ±.147	1.065 ±.654	0.090 ±.053	1.266 ±.087	0.276 ±.170	0.002 ±.002
8	1.231 ±.107	0.022 ±.003	0	1.277 ±.073	0.859 ±.221	0.122 ±.065	1.143 ±.057	0.910 ±.559	0.199 ±.118	--	0.416 ±.260	0.001 ±.001
10	0.799 ±.135	0.001 ±.004	0.004 ±.004	0.373 ±.131	0.889 ±.220	0.149 ±.070	--	0.859 ±.515	0.283 ±.168	0.981 ±.071	0.624 ±.389	0.002 ±.002
12	0.694 ±.089	0.105 ±.005	0.065 ±.062	0.983 ±.068	0.568 ±.167	0.072 ±.047	0.412 ±.183	1.611 ±.826	0.520 ±.341	0.656 ±.347	0.340 ±.297	0.003 ±.003
14	0.771 ±.148	0.218 ±.041	0.046 ±.036	0.185 ±.118	0.801 ±.155	0.250 ±.112	--	1.241 ±.473	1.149 ±.589	1.195 ±.306	1.021 ±.587	0
16	0.203 ±.068	0.290 ±.135	0.019 ±.013	0.383 ±.075	0.742 ±.124	0.375 ±.118	0.188 ±.087	1.456 ±.435	1.309 ±.592	0.346 ±.204	0.927 ±.479	0
18	0.143 ±.080	0.474 ±.216	0.007 ±.007	0.062 ±.056	3.851 ±.009	1.155 ±.072	--	1.134 ±.383	0.660 ±.363	--	0.973 ±.492	0.004 ±.002
20	0.108 ±.081	0.788 ±.334	0.018 ±.004	0.089 ±.027	0.901 ±.167	0.577 ±.166	0.052 ±.036	1.076 ±.259	0.647 ±.293	0.602 ±.212	0.681 ±.624	0.012 ±.007