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Field simulation of wet and dry years in the Chihuahuan desert: soil moisture, N mineralization and ion-exchange resin bags

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Abstract Irrigation and rain-out shelters were used to simulate precipitation patterns of wet and dry years in the northern Chihuahuan Desert. Irrigation provided approximately double the long-term average monthly precipitation. Rain was excluded during the wet season, July–October, to simulate a dry year. N net mineralization in laboratory incubations was undectable at calculated water potentials less than -1 MPa. With increasing moisture, mineralization gradually rose to the highest observed rates near field capacity. There was no mineralization maximum at moisture contents below field capacity. Irrigation significantly increased the water potential and rainfall exclusion reduced water potentials to less than -8 MPa. The general absence of important irrigation effects may have resulted from the high natural precipitation during the experiment or because irrigation inputs were insufficient to increase microbial activity during very dry periods. Precipitation exclusion reduced ion capture during the warm-wet season. After allowing precipitation inputs to resume, NH_4^+-N capture was increased in the cool-dry seasons of both 1987–1988 and 1988–1989. NH_4^+-N capture more than doubled that predicted from the overall covariance of moisture input and ion capture, suggesting increased availability of N. An unusually hot, dry period in May and June 1989 was followed by a three- to fourfold increase in the warm-wet season $NO_3^- + NO_2$-N capture compared to 1988. These data suggest that short droughts of about 3 months in length (both simulated and natural) increased N availability relative to moisture availability.

Key words *Larrea tridentata* · Simulated rainfall · Precipitation exclusion · Soil drying effects · Analysis of covariance · Chihuahan Desert · Mineralization rate · Field capacity

Introduction

Plant growth in the northern Chihuahuan Desert appears to be regulated by a dynamic relationship between the availability of water and N (Fisher et al. 1987, 1988). The general effects of variations in moisture availability on N availability are known from results obtained from laboratory incubation of soils collected from irrigated plots. These indicate that continuously wet conditions lead to a depletion of mineralizable N (Fisher et al. 1987). Oven-drying soils prior to incubation has led to small increases in mineralization rates, probably because of increased turnover of microbial biomass and native soil organic matter. A simple restatement of these results is that moist conditions deplete available N while dry conditions increase it. Moisture availability in many arid and semi-arid environments is better characterized as highly variable rather than simply as low. The coefficient of variation for precipitation in arid ecosystems is usually far higher than that of mesic ecosystems, and periods of surplus moisture do occur (Noy-Meir 1973; Hadley and Szarek 1981; Ludwig 1987). Generalizations based upon the imposition of simple, continuous experimental treatments, such as regular irrigation, must be extrapolated to complex patterns of moisture inputs and drought.

Our previous study used only laboratory incubations of soil collected at a single point in time in a dynamic, constantly changing ecosystem (Fisher et al. 1987). A quantitative understanding of water/N relationships requires the use of methods to measure in-situ N availability over a period of time. Integrative measures of soil processes over seasons or years are needed to complement data collections from a single point in time.

The use of ion-exchange resin bags holds promise for the in-situ measurement of N availability. These bags are

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incubated in the soil profile for periods of time and collect $NO_3^- + NO_2^-$-N or NH_4^+-N moving through the profile. Capture of ions by ion-exchange resin bags depends upon N mineralization rates, ion form ($NO_3^- + NO_2^-$-N or NH_4^+-N), water movement to the bags, and competition for ions with soil microorganisms and plants (Binkley and Hart 1989). Since these are the same factors affecting the availability of N to plants, the bags provide a useful index of soil N availability, and have been used to compare treatments and ecosystems in forests (studies cited by Binkley and Hart 1989) and deserts (Lajtha 1988). The major weakness of ion-exchange resin bags is that it is difficult to identify which of the several factors is responsible for observed differences (Binkley and Hart 1989).

Here we present data resulting from the use of ion-exchange resin bags in an experiment examining the influence of moisture availability on soil N availability in a northern Chihuahuan Desert ecosystem. Irrigation and rain-out shelters were used to simulate precipitation patterns from wet and dry years in order to test the predictions that (1) increased moisture availability would first increase and then decrease N availability because of N immobilization by microbial biomass, and (2) that decreased moisture availability would increase N availability because of death and mineralization of microbial biomass. The irrigation was calibrated to bring moisture input up to a predetermined amount typical of a wet year as determined from past precipitation records. This incorporated the seasonality of precipitation in the Chihuahuan Desert, an important source of variation. Precipitation was excluded during the July–October wet season to simulate a dry year. A variety of laboratory and in-situ measurements related to soil N availability were taken, but only those related to the ion-exchange resin bags are presented here. In addition, we report the effects of the treatments on soil water potential and, to link the soil water potential data to the N-availability data, we characterized the response of N mineralization to moisture availability in laboratory incubations.

The experimental manipulation of moisture availability is a way of quantifying the overall response of ion-exchange resin bags to moisture inputs. An analysis of covariance is then used to compare the response by the bags to known moisture inputs for different treatments and incubation times. This in turn extends the ability to interpret the resin bag results, and therefore, the effects of the experimental treatments.

Materials and methods

The study was conducted at the Jornada Long-Term Ecological Research (LTER) site located 40 km NNE of Las Cruces, New Mexico, on a northeast-facing piedmont in a shrubland dominated by creosotebush [*Larrea tridentata* (DC.) Cov.]. The creosotebush zone is located on a midslope (3% gradient) on loamy sand soils with a calcium carbonate deposition layer (caliche) at ca. 40 cm. The soil is classified as a Typic Haplargid of the Doña Ana series (Wierenga et al. 1987). Total N and organic C at 0–10 cm average 400–500 and 5000–6000 mg kg^{-1}, respectively, under shrubs, and 200–400 and 3000–5000 mg kg^{-1}, respectively, between shrubs. Annual precipitation averages 213 mm, 55% falling during July–September as convectional thunder-showers. Temperatures regularly exceed 40 °C in summer and regularly fall below 0 °C during winter nights. The northern Chihuahuan Desert climate can be conveniently characterized as consisting of three seasons, the warm-wet season, from July to November, the cool-dry, from December to March, and the warm-dry, from April to June. Precipitation falling during the warm-wet season is transpired fairly rapidly. In contrast, precipitation falling during the cool-dry season beginning in December is normally stored until it is transpired early in the warm-dry season. The latter season is characterized by progressively drier conditions leading to the hottest days of the year in June. The onset of monsoonal moisture flows from the tropics leads to cooler temperatures and convective thunderstorms in the warm-wet season.

The experimental plots consisted of 24 3×5-m plots, each with at least two shrubs with a total canopy area of at least half the plot. Three treatments (control, dry, wet) were assigned to the plots in a completely random manner within constraints imposed by routing irrigation pipes, excluding runon from drought plots, and avoiding runoff from irrigation plots. This provided eight "drought", eight irrigated, and eight control plots. Soil water potentials were monitored in each plot at regular intervals using Wescor (TM) soil psychrometers placed at 5 and 15 cm depths. Irrigation amounts were determined by comparing the target with running totals every 2 weeks. The target amount for each 2-week period was to apply the greater of (1) 6.35 mm water, or (2) double the amount of the long-term monthly mean, resulting in a total annual moisture input of 475 mm. Since a minimum of 6.35 mm water was applied every 2 weeks, the resulting moisture inputs were somewhat greater than the target amount of 475 mm. Irrigation was applied weekly or biweekly by pumping water from a mobile tank through a sprinkler system elevated above shrub canopy height (Fisher et al. 1988). The irrigation amounts were verified using containers placed in the ground in open areas. Rain-out shelters were constructed of a steel frame (1.5 m on the sides and 2.2 m at the roof peak). Shelter frames were built over the eight plots assigned to drought but there were no frames around the irrigation and control plots. Ultraviolet light-resistant greenhouse polyethylene attached to the center beam of the roof was rolled down over the roof to exclude rain. Because the roofs were rolled down only when storms approached or at night, no temperature or humidity differences arose from the presence of the rain-out shelters. Details on construction of rain-out shelters are available from the authors.

All samples were located in plots using random-number tables to select shrubs and then to select one of eight directions (N, NE, E, SE, S, SW, W, NW) from the base of the shrub. Locations of poor treatment effectiveness, such as the corners of irrigated plots farthest from the sprinklers, were avoided. Ion-exchange resin bags (anion and cation) were placed both under and between shrubs at a 10-cm depth. Three incubation periods of variable length were chosen each year to characterize conditions of the three seasons (warm-dry, warm-wet, and cool-dry).

An analysis of variance was applied to the data, with incubation location (canopy, open) nested within three randomly assigned treatments (contol, dry, wet). The error term for treatment effects therefore consists of the treatment×plot interaction ($7 \times 2 = 14$ *df*; Steel and Torrie 1980). Our a priori expectations were that all three treatments would differ and that treatment effects would differ between canopy and open locations. We therefore planned contrasts accordingly. Residuals for all analyses were examined for heterogeneous variances by plotting against predicted values and for departures from normality using the Shapiro-Wild W statistic (SAS Institute Inc. 1985). These procedures indicated that log transformations [$\ln(X+0.1)$] were needed to correct heterogeneous variances.

Ion-exchange resin

Resin bags were constructed of unbleached, tubular nylon stocking material obtained from L'eggs Products, Inc., Mesilla Park, NM. The material selected for use was relatively hydrophilic and had a mesh size small enough to prevent loss of resin. Approximately 8 g dry mass of Dowex 1-X8 anion exchange resin or Dowex 50W-X8 cation exchange resin was placed in 12-cm lengths of stocking material and sewn closed at both ends, giving bags with a 50-cm^2 area. Anion and cation bags were charged by three successive washes of 0.5 *M* $NaHCO_3$ or 0.5 *M* HCl, respectively (Lajtha 1988), and then excess water was removed centrifugally with a salad spinner. The completed resin bags were refrigerated at 3–5 °C until use. No bags contained both anion and cation resin because the mixed resin could have interfered with automated colorimetric techniques for the determination of inorganic N.

The resin bags were placed in holes at the 10-cm depth, covered with the soil removed from the hole, and left in place for varying lengths of time (Table 1). Ion-exchange resin bag comparisons were made using bags treated in the same way in control and treatment plots. Contamination during preparation and installation was estimated by using resin bags transported to the field with sample bags and then returned to the lab and refrigerated (field blanks). Field blank values were subtracted from the values for all experimental bags. Field blanks indicated high levels of $NO_3^- + NO_2^-$-N contamination in one set of incubations (warm-wet 1989) and these data are not reported.

Collected resin bags were rinsed with deionized water to remove adhering soil and excess water was again removed centrifugally. Ions were extracted by submerging the intact bags in 100 ml 2.0 *M* KCl overnight followed by filtration through Whatman no. 42 paper. Resin collected in filters was oven-dried (50 °C) and the mass determined. NH_4^+-N was measured in the extracts by an automated salicylate procedure (Wall and Gehrke 1975; Nelson 1983) and $NO_3^- + NO_2^-$-N was measured by an automated Cd reduction procedure (Henriksen and Selmer-Olsen 1970).

Statistical analysis of moisture inputs

We compared the effect of total moisture inputs to the experimental plots with the treatment effects of irrigation and precipitation exclusion by using analysis of covariance. This analysis seeks to answer the question "Are there treatment effects that cannot be explained by quantity of moisture input alone?" Other important quantifiable factors expected to influence ion capture were the duration and season of the ion-exchange resin bag incubations. However, the variations due to incubation duration and to incubation season were confounded; longer incubations were performed during the cool-dry winter. Therefore, we performed two separate analysis, one using soil moisture input, treatment effects, and incubation duration; and a second using soil moisture input, treatment effects, and incubation season.

The analysis was performed using treatment means as replicates. The residuals of the analysis are the appropriate error term because they are the deviations of experimental means from the model. Treatment means from a series of sample collections should fail the assumption of independence of errors because of autocorrelation through time. This was apparent in plots of the residuals vs. date, mostly because of differences between years. However, the effect of the violation of this assumption is to inflate error estimates. Therefore, in the interests of maintaining a conservative analysis, no additional effort was made to correct this.

The analysis was performed essentially as a stepwise backward-elimination multiple regression analysis. An initial model was calculated containing treatment, season, treatment × season interactions, moisture inputs, and moisture input interactions with treatment and season. Non-significant variables were then eliminated in a stepwise manner at $P > 0.05$ with the exception of treatment effects which were included in all models. This made the models more conservative by reducing degrees of freedom. Factors containing the category variables treatment or season were eliminated as a group. Residuals of all analyses were examined for heterogeneous variances and for outlying values that might excessively weight the results.

Incubation experiment

The response by soil N mineralization to varying soil moisture contents was examined in a laboratory incubation experiment. Soil was collected in January 1988 from a location adjacent to the study plots from a previous irrigation/fertilization experiment (Fisher et al. 1987, 1988). Composite soil samples were obtained from the canopy and open areas around five shrubs located far enough from the plots to be unaffected by the previous study. The soils were air-dried and then incubated for 8 weeks at 35 °C in plastic vials covered with four layers of 0.5 ml polyethylene pierced by a single hole to accommodate moisture additions with a syringe (Fisher et al. 1987). Soil moisture was adjusted weekly by mass to proportional moisture contents (105 °C) of 0.04, 0.06, 0.08, 0.10, or 0.12 (field capacity). An additional group of samples received no moisture additions. All samples, including those receiving no moisture, were shaken after each moisture addition to distribute the moisture evenly in the soil. Losses of moisture for samples adjusted to 0.06 moisture content or

Table 1 Comparison of moisture inputs (precipitation + irrigation) and durations of resin-bag incubations in the experimental plots to total moisture inputs and the total time available to perform incubations (time interval between sample collections). Rain was excluded at intervals during the warm-wet season. The two dates at the head of each column represent burial date followed by retrieval date

Treatment or time interval	Warm-dry season			Warm-wet season			Cool-dry season	
	5/6/87 to 7/29/87	5/3/88 to 6/30/88	5/3/89 to 6/28/89	8/25/87 to 10/13/87	6/30/88 to 10/25/88	6/28/89 to 10/24/89	10/28/87 to 3/30/88	12/6/88 to 5/3/89
Moisture inputs to treatment plots during incubation (mm)								
Control	79.8	29.0	9.0	14.2	220.0	205.4	88.9	71.9
Dry	79.5	29.0	9.0	0.0	0.0	0.0	88.9	71.9
Wet	136.9	60.7	53.5	58.7	283.5	326.0	146.1	116.3
Total moisture inputs during time intervals between sample collections (mm)								
Control	79.8	40.6	9.0	69.8	220.0	205.4	91.2	79.8
Dry	79.5	40.6	9.0	0.0	0.0	0.0	90.2	79.5
Wet	136.9	85.1	53.5	202.2	283.5	326.0	172.7	156.3
Incubation duration and total time intervals between sample collections (days)								
Incubation duration	84	58	56	49	117	118	154	148
Total interval	84	92	56	76	117	118	169	190

higher averaged about 0.01 per week. Subsamples were removed at weeks 1, 2, 4, and 8 for determination of the oven-dry moisture content and $NO_3^- + NO_2^-$-N and NH_4^+-N by methods described above.

Results

Moisture

Precipitation during the period of the experiment generally exceeded long-term averages except during the latter part of the cool-dry season of 1988–1989 and the warm-dry season of 1989. Patterns of precipitation differed between the 3 years of the study; 1987 had relatively few events but several in June, July and August were quite large, exceeding 40 mm (Fig. 1). The wet seasons of 1988 and 1989 were characterized by small, frequent rain events. The warm-dry season of 1989 was hotter than 1987 or 1988, and only 9 mm of precipitation was recorded from 03 May 1989 to 30 June 1989 (Table 1). The overall patterns of 1988 and 1989 were very similar, differing mainly during May–June, when 1989 was hotter and drier.

Water potentials in the control plots ranged from less than −8 to 0 MPa during the experiment (Fig. 2). Irrigation significantly increased the water potential but, when control plots were very dry, water potentials in irrigated plots ranged from −6 to −4 MPa. Precipitation exclusion significantly reduced the water potential less than −8 MPa (Fig. 2).

Laboratory incubations

Relative N mineralization responses to the manipulation of soil moisture content in laboratory incubations were consistent for canopy and open soils throughout the 8-week period of the incubation (Fig. 3). Mineralization was undetectable at water potentials calculated to be less than −1 MPa. With increasing moisture, mineralization gradually rose to the highest observed rates near field capacity (0.12 oven-dry mass, ≈0 MPa) with no sign of a

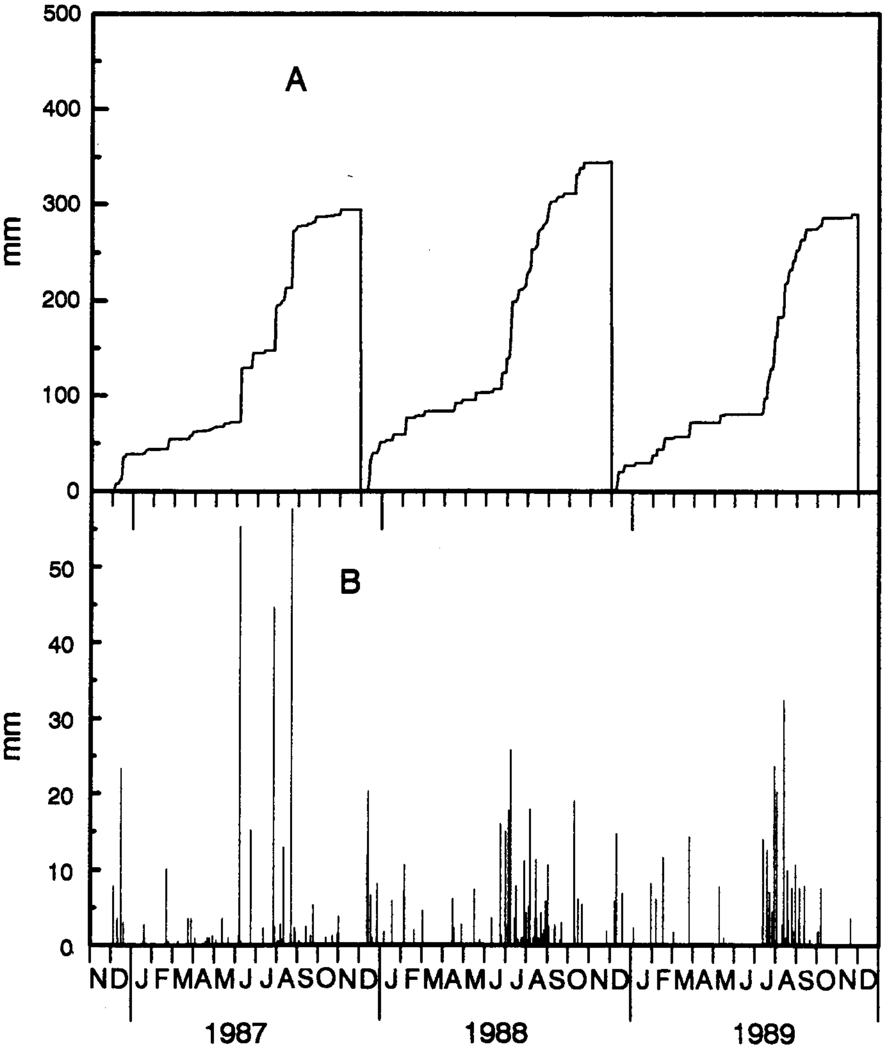
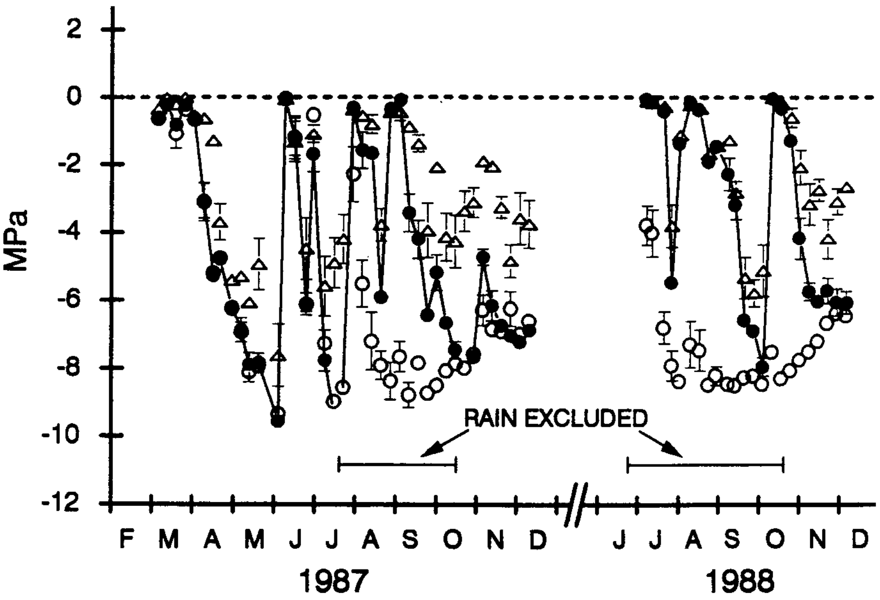


Fig. 1A, B Precipitation during the study: **A** Cumulative annual precipitation. Annual accumulation is calculated from 1 December because this precipitation is used during the following spring. **B** Precipitation events during the study

Fig. 2 Soil moisture responses to irrigation (*WET* △) and precipitation exclusion (*DRY* ○). Values are means from soil psychrometers at 5 and 15 cm for eight treatment plots. Error *bars* are 2 SEM, ●——● control



mineralization maximum at moisture contents below field capacity.

Ion-exchange resin bags

The incubation periods of the ion-exchange resin bags included most of the precipitation during the experiment (Table 1). With the exception of the first warm-wet season incubation, from August to October 1987, all incubations included more than 70% of the total precipitation plus irrigation. One hundred percent of the available moisture input was included in four of the eight incubations. The first warm-wet season incubation, from August to October 1987, sampled less than 30% of the moisture inputs during the season, and therefore may not be representative.

The $NO_3^- + NO_2^-$-N capture by the ion-exchange bags in response to irrigation or precipitation exclusion was greater under shrub canopies than in open areas between shrubs (Table 2). There was considerable variation in $NO_3^- + NO_2^-$-N absorption between years, especially during the warm-wet season.

$NO_3^- + NO_2^-$-N capture did not show consistent statistically significant responses to irrigation, even during the warm-dry season (Table 2). However, mean $NO_3^- + NO_2^-$-N capture levels in irrigated plots were about twice those in control plots in canopy soils during the warm-dry and warm-wet seasons of 1987 ($P = 0.053$, $P = 0.092$), the cool-dry season of 1987–1988 ($P = 0.18$), and the warm-wet season of 1989 ($P = 0.35$). Overall, the consistently higher means found in irrigated samples during 1987 and early 1988 strongly suggest that $NO_3^- + NO_2^-$-N capture did respond to irrigation but the response was too small to be readily detected under this experimental design.

Precipitation exclusion during the warm-wet season resulted in the largest treatment response, significantly reducing $NO_3^- + NO_2^-$-N capture by the resin bags (Table 2). There was some indication of residual effects from the dry treatment after the rain-out shelter was removed in the cool-dry season; $NO_3^- + NO_2^-$-N capture tended to be higher under shrub canopies in dry plots than in controls during the 1987–1988 cool-dry season, and tended to be higher in open areas between shrub canopies during the 1988–1989 cool-dry season.

NH_4^+-N capture by the resin bags exhibited greater responses to the experimental treatments under shrub

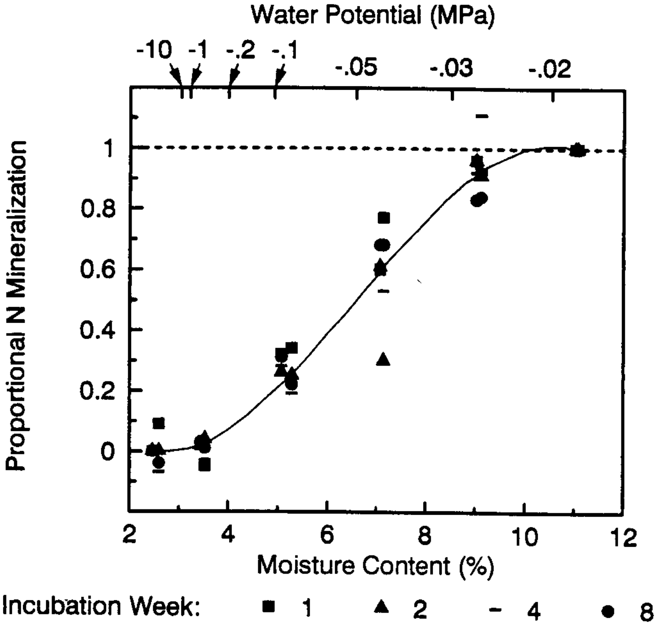


Fig. 3 Response of N net mineralization in 35 °C incubations to varying soil moisture contents. The equation for the fitted curve is: $N = 0.433 - 0.357 \times M + 0.0834 \times M^2 - 0.00421 \times M^3$ where N is proportional N mineralization and M is moisture content (%). Conversion of moisture content (%) to water potential (MPa) was accomplished with the equation of Schlesinger et al. (1987)

Table 2 Effects and statistical significance of rain exclusion (*Dry*) and irrigation (*Wet*) effects on $NO_3^- + NO_2^-$-N capture by ion-exchange resin bags buried at 10-cm soil depth for the time intervals indicated (see Table 1 for further explanations)

Soil and treatment/ contrast	Warm-dry season			Warm-wet season			Cool-dry season	
	5/6/87 to 7/29/87	5/3/88 to 6/30/88	5/3/89 to 6/28/89	8/25/87 to 10/13/87	6/30/88 to 10/25/88	6/28/89 to 10/24/89	10/28/87 to 3/30/88	12/6/88 to 5/3/89
Canopy soils [mg $NO_3^- + NO_2^-$-N (10 g resin)$^{-1}$]								
Control	1.55	0.78	–	0.27	5.4	13.8	0.99	4.20
Dry	1.83	0.56	–	0.03*	0.52*	1.13*	3.13	3.08
Wet	2.98	1.01	–	0.67**	5.37**	22.26**	2.42	4.12
Open soils [mg $NO_3^- + NO_2^-$-N (10 g resin)$^{-1}$]								
Control	1.03	0.81	–	0.26	1.31	4.71	0.00	0.16
Dry	1.01	0.64	–	0.04*	0.64	2.06	0.09	1.08*
Wet	1.26	0.89	–	0.29**	1.00	3.42	0.04	2.38*

*$P < 0.05$ vs. control; **$P < 0.05$ vs. dry

canopies than in open areas. However, the annual variation in NH_4^+-N capture was somewhat less than for $NO_3^- + NO_2^-$-N (Table 3).

NH_4^+-N capture in the irrigated plots was significantly higher than controls during the unusually hot and dry warm-dry season of 1989. Unfortunately, no $NO_3^- + NO_2^-$-N data from this period are available for comparison.

Like $NO_3^- + NO_2^-$, NH_4^+-N capture was reduced by precipitation exclusion during the warm-wet season (Table 3). Significantly more NH_4^+-N was captured in dry-treatment bags during the cool-dry season after removal of the rain-out shelters. This residual affect of precipitation exclusion was much stronger than the $NO_3^- + NO_2^-$-N trends reported above.

The overall levels of NH_4^+-N were surprisingly high compared to $NO_3^- + NO_2^-$-N, often being similar, and occasionally higher (Tables 2, 3). The lowest ratios of $NO_3^- + NO_2^-$-N to NH_4^+-N were found in samples that had been in the field only a short time and/or had very low moisture inputs because of precipitation exclusion.

Moisture and ion-exchange resin bag relationships

The analyses of covariance for field treatment, moisture input during incubation, and duration of incubation explained 77% or more of the variation in NH_4^+-N and $NO_3^- + NO_2^-$-N capture. However, these models were very sensitive to one particularly low value, the dry treatment during the warm-wet season of 1987. The removal of this value from the model caused significant changes, casting some doubt about the reliability of these models, and they are not discussed further.

The analyses of covariance for field treatment, moisture input during incubation, and season of incubation explained 75% or more of the variation in NH_4^+-N and $NO_3^- + NO_2^-$-N capture (Table 4). Overall, these models are described by the equation:

$$\text{Captured N} = [\text{Intercept} \times \exp(a \times \text{moisture})] - 0.1$$

where a is the slope parameter of moisture input. The models consist of none or more curves, with each individual curve indicating the response to moisture inputs for a different combination of treatment and incubation season. On a log scale, the curves appear as parallel lines and the effects of experimental treatments and incubation seasons produce different intercepts (Figs. 4, 5).

Analysis of $NO_3^- + NO_2^-$-N capture was complicated by differing responses during the warm-wet seasons of 1988 and 1989. Eliminating the data from the warm-wet season of 1988 resulted in the simplest model (Table 4, Fig. 4). The only significant factor in this model was the moisture-input slope; the experimental treatments did not significantly increase the explained variance for this subset of the data. This model is therefore reduced to a sim-

Table 3 Effects and statistical significance of rain exclusion (*Dry*) and irrigation (*Wet*) effects on NH_4^+-N capture by ion-exchange resin bags buried at 10-cm soil depth for the time intervals indicated (see Table 1 for further explanations)

Soil and treatment/ contrast	Warm-dry season			Warm-wet season			Cool-dry season	
	5/6/87 to 7/29/87	5/3/88 to 6/30/88	5/3/89 to 6/28/89	8/25/87 to 10/13/87	6/30/88 to 10/25/88	6/28/89 to 10/24/89	10/28/87 to 3/30/88	12/6/88 to 5/3/89
Canopy soils [mg NH_4^+-N (10 g resin)$^{-1}$]								
Control	1.47	0.70	0.93	0.67	1.90	3.78	0.69	0.79
Dry	1.74	0.42	0.65	0.32	0.81*	1.04*	2.14*	2.24*
Wet	2.25	0.86	1.94*,**	0.56	2.21**	3.81**	0.75**	0.91**
Open soils [mg NH_4^+-N (10 g resin)$^{-1}$]								
Control	1.13	0.12	0.44	0.05	0.61	0.71	0.16	0.65
Dry	0.82	0.27	0.30	0.02	0.48	1.09	0.62*	1.03
Wet	1.06	0.18	0.62**	0.08	0.97	1.32	0.20**	0.64

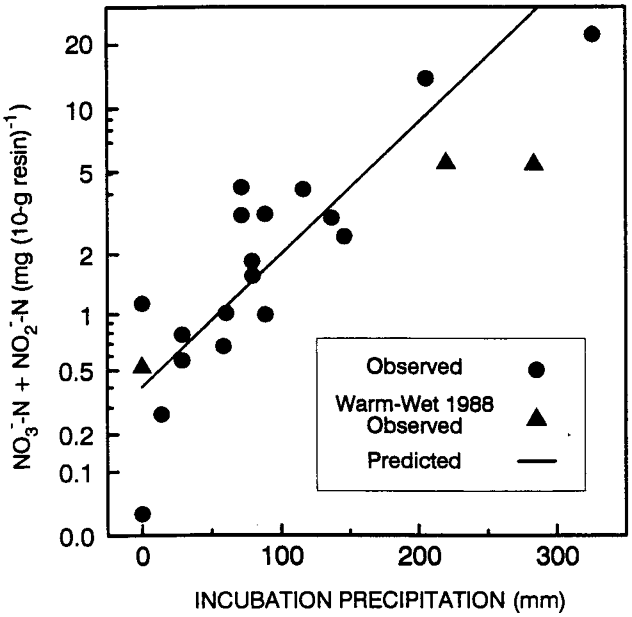


Fig. 4 Relationship between precipitation and NO_3^- + NO_2^--N capture by ion-exchange resin bags buried at 10-cm depth under shrub canopies. Data points from warm-wet season of 1988 were excluded from the analysis of covariance. $R^2 = 0.75$ for fitted analysis of covariance model

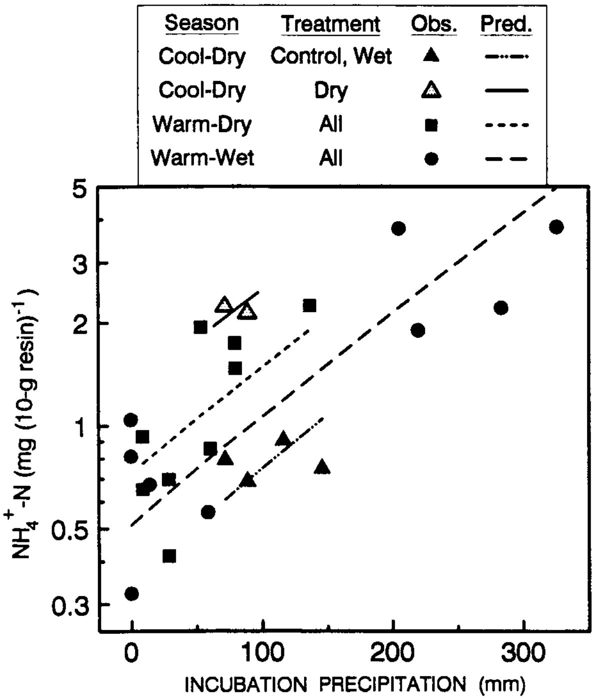


Fig. 5 Relationship between precipitation, season, experimental treatment, and NH_4^+-N capture by ion-exchange resin bags buried at 10-cm depth under shrub canopies. $R^2 = 0.79$ for fitted analysis of covariance model. Precipitation exclusion (*Dry*) was significantly different from the irrigated (*Wet*) and control treatments during the cool-dry season ($P < 0.01$). *Obs* observed, *Pred* predicted

ple linear regression of ln(NO_3^- + NO_2^--N)-0.1 vs. moisture input. The data from warm-wet 1988 showed a reduced response to high moisture inputs compared to the model predictions.

The NH_4^+-N model was similar to the NO_3^- + NO_2^--N model in that moisture input explained much of the variation (Table 4, Fig. 5). NH_4^+-N differed from NO_3^- + NO_2^--N in that there was little difference in the response between the warm-wet seasons of 1988 and 1989. The other major feature of the NH_4^+-N model was a significant treatment × season interaction. This appears to indicate that during the cool-dry season, the dry treatment led to a higher NH_4^+-N capture at a given moisture input than the control or wet treatments. The predicted dry-treatment NH_4^+-N capture for a given moisture input during the cool-dry season was more than double that for the control and wet treatments.

Discussion

Irrigation effects

Overall ion capture by ion-exchange resin bags is likely to follow moisture inputs because of (1) the importance of moisture in transporting ions to the resin (Binkley and Hart 1989) and (2) the direct effects of soil water potential on microbial activity and N mineralization. Since moisture availability was manipulated by the experiment, any simple comparison of treatment-effect means is likely to be overwhelmingly influenced by these two factors.

We predicted that irrigation would initially increase and then decrease N availability and that precipitation exclusion would increase N availability. To use ion-exchange resin bags to detect moisture effects, we used analyses of covariance to statistically control for the moisture effects on ion movement. By quantifying the overall response of ion capture to moisture, which is primarily a result of the direct effects of moisture on transport and microbial activity, differences resulting from other factors will be revealed as differing responses (slopes, intercepts) to moisture inputs. The analysis of covariance for ion-exchange data cannot identify which factors, such as changes in the quantity and quality of mineralizable organic N, are responsible, but it can suggest particular instances where such differences are likely to be found.

Irrigation was predicted to initially increase soil N availability followed by a decrease as mineralizable N was depleted by rapid microbial activity. The initial increase would increase the slope or intercept in analysis of covariance models of ion capture vs. moisture inputs and the mean ion capture would significantly exceed that in irrigated and control plots. The subsequent decrease in mineralizable N should decrease the slope and/or intercept. However, the mean ion capture in irrigated plots could conceivably still exceed that in controls due to the strong influence of moisture inputs on transport and microbial activity. Therefore, mean ion capture is not par-

Table 4 Overall results and parameter estimates (slopes and intercepts) from analysis of covariance of treatment (control, dry, wet), incubation season, and estimated moisture input on ion capture by ion-exchange resin bags. The resulting models are described by the general equation:
captured N = [intercept·exp (*a*·moisture)] − 0.1
where *a* is the slope of moisture input. Ions are transformed to $\ln(X+0.1)$. The analysis was performed upon subsets of $NO_3^- + NO_2^-$-N depending upon whether relatively low or high $NO_3^- + NO_2^-$-N was observed during the warm-wet seasons of 1988 to 1989. Letters indicate significantly different NH_4^+-N intercepts ($P<0.05$)

Source of variation	Ion (data subset)	
	NH_4^+-N (all data)	$NO_3^- + NO_2^-$-N (w/o 1988 warm-wet)
Overall results		
Model R^2	0.79	0.75
F (model *df*, error *df*)	5.7 (9, 14)	13.7 (3, 14)
Model *P*	0.002	<0.001
Moisture input slope (mm^{-1}) (1 *df*)		
Moisture slope	0.0065**	0.0144**
Treatment intercepts [mg N (10 g resin)$^{-1}$] (2 *df*)		
Control treatment intercept	0.66AB[a]	0.56
Dry treatment intercept	0.90A[a]	0.59
Wet treatment intercept	0.55B[a]	0.39
Season intercepts [mg-N (10 g resin)$^{-1}$] (2 *df*)		
Warm-wet season intercept	0.61	–
Warm-dry season intercept	0.83	–
Cool-dry season intercept	0.64	–
Treatment-season interaction intercepts [mg-N (10 g resin)$^{-1}$] (4 *df*)[b]		
Control treatment cool-dry season	0.50B	–
Dry treatment cool-dry season	1.36A	–
Wet treatment cool-dry season	0.39B	–

[a] These results are confounded by a significant treatment × season interaction

[b] Only treatment × season interaction parameters from significant contrasts are shown

ticularly useful in detecting reductions in mineralizable N unless the reductions are very large. The conclusion that the original hypothesis should be rejected is not supported by the laboratory incubations and previous work (Fisher et al. 1987) as discussed below.

The observed irrigation effects on mean ion capture were generally small or inconsistent, with the strongest effects occurring during the first year of the experiment. Irrigation caused no detectable effects on the slope or intercept of the ion-capture responses to moisture input, indicating that the effects of irrigation were generally limited to the direct effects of moisture inputs on transport and microbial activity. The absence of important irrigation effects on soil mineralizable organic N is supported by measurements of mineralization potential in laboratory incubations (F.M. Fisher 1989, unpublished data).

The absence of a response to irrigation apparently conflicts with results of a previous study showing large reductions in mineralizable organic N resulting from irrigation (Fisher et al. 1987). However, in the previous study, more moisture was added in a different seasonal pattern for a longer period of time. Annual irrigation in the present study ranged from 180 to 240 mm compared to about 300 mm in the previous study. In the present study, most moisture was added during warm seasons when evapotranspiration was very rapid, whereas in the previous study, moisture was added equally throughout the year (see below). Also, annual precipitation was above the average of 213 mm in every year of the present study, reducing the likelihood of any responses to additional moisture. Finally, the results reported here are from the first 3 years of the experiment while the results reported previously were from the 5th year of the experiment.

Performing most of the irrigation during the warmer periods of the year may significantly reduce irrigation effectiveness. Natural precipitation events are accompanied by cloudy and cooler conditions that reduce evapotranspiration. Figure 2 shows that natural precipitation events increase the water potential to nearly 0 MPa for sustained periods of several days to a week during July and August. In contrast, irrigation during hot sunny days may increase the water potential 24 h after irrigation to only −4 MPa. In the previous study (Fisher et al. 1987, 1988), more moisture was added during cool seasons, which raised the water potential to nearly 0 MPa. Moreover, cool-season soil temperatures are high enough to support significant microbial activity.

The laboratory-incubation response by N mineralization to varying moisture contents helped in the interpretation of the effects of irrigation on ion capture. The results of the present laboratory incubations differed from similar studies (Stanford and Epstein 1974; Cassman and Munns 1980) in that (1) essentially no inorganic N accumulated under relatively dry conditions and (2) a peak mineralization rate was absent under wet conditions. This soil has relatively low organic C and total N concentrations, but they are well within the ranges of the soils used in other moisture manipulation studies (Stanford and Smith 1972; Stanford and Epstein 1974; Cassman and Munns 1980). However, the texture of this soils, a loamy sand, is considerably coarser than any of the soils in the previous studies, which were silty loams or silts.

Soil texture is well known to influence microbial responses to drying. Microbial populations in dry soils are thought to be largely limited to clay surfaces (Stotzky 1972). Clays may also protect microbial cells during drying (Van Veen et al. 1984). The low clay content of a loamy sand soil, compared to silt loams or silts, may result in low levels of protected microbial biomass, and hence N mineralization, under dry conditions. Rates of diffusion through a sandy soil are very slow at low moisture contents, so organisms are essentially starved (Swift et al. 1977; Davidson et al. 1990). Our findings of low N mineralization rates under dry conditions are not restricted to laboratory incubations; buried bag incubations (Binkley and Hart 1989) during the warm-dry season also showed negligible N accumulation (F.M. Fisher 1989, unpublished data).

The significance of the moisture response incubations is the demonstration that using irrigation to raise the soil water potential from −9 to −4 MPa had little effect on soil microbial activity. Overall, the results of this study suggest targeted irrigation treatments should be based on some other factor besides moisture inputs, such as soil moisture content or soil water potential.

Precipitation exclusion and annual variation

We predicted that precipitation exclusion would increase ion capture during subsequent periods of adequate moisture as a result of increased availability of mineralizable organic N. (Decreased ion capture during the warm-wet season moisture exclusion was expected because of slow microbial activity and lack of moisture transport. However, this is a trivial result.) During periods of adequate moisture following moisture exclusion, increased mineralizable N availability was expected to increase the slope and/or intercept in the analysis of covariance models of N capture vs. moisture inputs. This was observed for NH_4^+-N during the cool-dry seasons of 1987–1988 and 1988–1989. A number of other factors can influence ion capture, including organic matter inputs from creosotebush litter and annual plants, and competition for ions from plant roots or microorganisms. However, laboratory soil incubations suggested that N availability was increased in dry treatment soils (F.M. Fisher et al., unpublished data).

One of the largest responses was the difference in $NO_3^- + NO_2^-$-N capture during the warm-wet seasons of 1988 vs. 1989. This necessitated the exclusion of the warm-wet season of 1988 from the $NO_3^- + NO_2^-$-N analysis of covariance model (Fig. 4). The resulting model uses $\ln(NO_3^- + NO_2^-\text{-N})$, implying that logarithmic increases of ion capture were associated with linear increases in moisture input. However, the responses, including warm-wet 1988, can be modelled without log-transforming the data (a linear response). The linear relationship during the warm-wet 1988 season can be produced by the direct effects of moisture transport on ion capture or by substrate limitation of microbial activity at higher moisture inputs. In contrast, the warm-wet 1989 season data require a log transformation to be adequately modelled. At the same moisture content, $NO_3^- + NO_2^-$-N in the warm-wet 1989 season resin bags was three to four times higher than in warm-wet 1988. These data suggest that overall N availability was much higher following the hot dry period in 1989.

A variety of mechanisms can account for the differing N availabilities in the warm, wet seasons of 1988 and 1989. A smaller $NO_3^- + NO_2^-$-N capture for a similar moisture input may result from (1) immobilization of N by microbes, (2) nutrient uptake by roots, (3) increased rates of denitrification, or (4) substrate limitation of microbial activity. Alternative 1, immobilization, was considered unlikely because although the biomass of spring (cool-dry season) annuals, which die and begin decomposing during the warm-wet season, was relatively high in 1988 (F.M. Fisher and W.G. Whitford 1989, unpublished data) before the warm-wet season of 1989, but the biomass N concentration was about 12 mg g^{-1}, much higher than the concentration thought to cause significant immobilization in this soil (Fisher et al. 1990). Alternative 2, root uptake, also appears unlikely. Root activity in the top 10 cm is largely limited to annual plants. Annual-plant production was similarly low during the warm-wet seasons of both years (F.M. Fisher et al. 1989, unpublished data) and therefore root uptake seems unlikely to account for the difference between 1988 and 1989. Alternative 3, denitrification, appears equally unlikely. In laboratory incubations to measure denitrification in soils of the study area, Peterjohn and Schlesinger (1991) flooded cores with the equivalent of a 31.5-mm rainstorm. The flooding of a core with a quantity of water greater than any storm recorded at the site in 20 years of rainfall records for the site cannot give a realistic measure of denitrification in the soils subjected to our experimental treatments. In addition the rates reported for the *Larrea* sp. shrubland soils were the lowest recorded by Peterjohn and Schlesinger (1991). Denitrification is therefore not an adequate explanation of the results of the present study.

Alternative 4, substrate limitation, appears to be the most likely. Two factors may have increased the substrate for available for N mineralization during 1989. One was the extreme warm-dry season of 1989. The unusual heat may have modified organic compounds in the soil or litter, making them more available (Fisher et al. 1987). A second factor is that the pulse of organic matter from the annual plants of the cool-dry 1988 season should have been sufficiently decomposed to cause net N mineralization (Fisher et al. 1990). The presence of increased substrate availability is supported by overall higher mineralization potentials found during 1989 compared to previous years (F.M. Fisher et al. 1989, unpublished data).

The fact that the effect of exceptionally hot warm-dry season of 1989 on inorganic N availability was larger than the dry treatment leads us to question the effectiveness of the dry treatment. The major difference between a true summer drought and the dry treatment lies in the effects of the polyethylene cover. Although overall air temperatures are warmer under the polyethylene canopy, humidity is higher and inputs of ultraviolet radiation (not measured) are probably lower. These factors may reduce changes in organic matter, particularly in litter exposed to light, thereby reducing the effectiveness of the dry treatment on organic substrates. Despite problems with the dry treatment, these data do suggest that short droughts of about 3 months in length, both simulated and natural, increased N availability relative to moisture availability.

General patterns

Generally greater responses to the experimental treatments were found for canopy soils than for open soils. This may reflect the overall higher rates of soil processes under shrub canopies (Parker et al. 1982; Virginia and Jarrell 1983). However, Fisher et al. (1987) previously found a number of responses in open areas. There are several possible explanations for this apparent inconsistency. First of all, the previous experiment involved a larger perturbation performed over a longer period of time so that the organic-matter poor open areas were more likely to yield detectable responses. Secondly, the open areas of larger plots used in the previous experiment were subjected to more foot traffic from sample collection. (Foot traffic is absent under shrubs.) In the present study, many routine sample collections, such as reading soil psychrometers, were performed from outside the plots. In general, the lack of response in the open areas seems entirely consistent with the mildness of the treatments and the lower levels of biological activity.

The overall patterns of ion capture are similar to those found in nearby sites by Lajtha (1988); ion capture was much higher in wet conditions than in dry and $NO_3^- + NO_2^-$-N capture was more sensitive to moisture than was NH_4^+-N. The ratio of NH_4^+-N : $NO_3^- + NO_2^-$-N was often > 1 during relatively dry periods in both this and in Lajtha's study. Although NH_4^+-N rarely accumulates in laboratory soil incubations, it does accumulate in field soils during dry periods (F.M. Fisher et al. 1987, unpublished data). The accumulation during dry periods may reflect a limitation of nitrification by slow diffusion of NH_4^+ to nitrifying bacteria (Davidson et al. 1990). NH_4^+-N may then be carried to the resin bags by occasional precipitation events.

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