Effects of Different Patterns of Supplemental Water and Nitrogen Fertilization on Productivity and Composition of Chihuahuan Desert Annual Plants

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ABSTRACT: The effects of supplemental water supplied as large events, 25 mm per month, or as frequent small events, 6 mm per week, and available nitrogen on density, aboveground biomass and species composition of an annual plant community were studied in the northern Chihuahuan Desert. The amendments of water and N had no effect on total annual plant density. However, supplemental water resulted in increased density of eight species and nitrogen fertilization produced increased densities in nine species. Total aboveground biomass was higher in the nitrogen fertilized plots; water amendments had no effect on dry matter production and there were no significant water-nitrogen interactions. Cluster analysis showed that species composition was similar on the fertilized plots and that the plots receiving 25 mm • month^{-1} additional water in a single event differed most from the others. Species richness was highest in the 6 mm • week^{-2}, unfertilized plots, and lowest in the unwatered-unfertilized plots. Biomass production of six of the 23 species recorded was significantly increased by nitrogen fertilization and biomass of two species was significantly reduced.

INTRODUCTION

Beatley (1974) suggested that in North American deserts, rainfalls of 25 mm or greater are necessary to trigger growth of annual herbs. Gutierrez and Whitford (1987) experimentally tested this hypothesis in the Chihuahuan Desert. They compared the effect of irrigating with 25 mm of water applied once each month with 25 mm of water applied in four, 6 mm, weekly irrigations on the biomass and density of annual herbs. Biomass and density of the relatively deep-rooted spring annuals were higher in the plots watered monthly than in the plots watered weekly, which partially supported Beatley's model. However, the shallow-rooted summer annuals were more abundant on plots watered weekly. As Sala and Lauenroth (1981) point out, small rainfalls account for a large proportion of the total rainfall in semiarid regions and their potential ecological importance has often been ignored.

Gutierrez and Whitford (1987) failed to find any relation between biomass or density of summer annuals and water amendments after 1 year of watering. They hypothesized that other factors were limiting plant growth and suggested that nitrogen was the primary limiting factor. Parker *et al.* (1984) provided additional evidence that nitrogen may be limiting in this system. They found a positive correlation between the nitrogen immobilized by fungi growing on dead roots and the annual plant biomass produced 4 months earlier.

Although considerable attention has recently been focused on the role of nitrogen as a factor limiting the growth of desert plants (West and Skujins, 1978; Skujins, 1981), many effects of both nitrogen and water, and the interaction between these factors on annual plants remain to be elucidated. Here we report the results of experiments designed to explore the effect of watering and nitrogen fertilization on the biomass, density and composition of annual herb communities in the Chihuahuan Desert.

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Study Area

The study area is located at the Jornada Long-Term Ecological Research Site on the New Mexico State University Experimental Ranch, 40 km NNE of Las Cruces, New Mexico (32°30'N, 106°45'N). This site is a desert watershed that empties into an ephemeral lake. The watershed varies in elevation from approximately 1300-1500 m. Our studies were conducted on the midslope area of the watershed where the perennial shrub vegetation is essentially monotypic *Larrea tridentata*, with other shrubs limited to the margins of drainages. The experimental plots were on *L. tridentata* uplands on sandy soils with a caliche layer (calcium carbonate deposition layer) between 0.7 and 1.0 m below the surface. Mean annual precipitation ± 1 SD is 211 ± 77 mm, with most rainfall occurring in late summer convectional storms. Maximum summer temperatures reach 40 C and freezing temperatures are recorded from October to mid-March (Houghton, 1972).

Methods

There were nine experimental plots, 7 x 15 m, in a split-plot design. Six plots were irrigated with the same total quantity of water. Three plots were watered weekly at 6 mm • wk^{-1} and three plots were watered once every 4th week with approximately 25 mm (monthly plots). Three plots received no irrigation. The plots were fenced to prevent herbivory by rabbits. The water amendments were initiated in 1981 and continued through 1984. On 23 February 1983 granular fertilizer (NH_4NO_3) was applied with a hand-held spreader at a rate of 100 kg N • ha^{-1} to the down slope half of each plot to prevent runoff of the added N onto unfertilized plots. Soil water potentials were obtained at irregular intervals using thermocouple psychrometers (Wescor model PCT 55-15-55, Logan, UT) at 5 cm and 15 cm depth.

Annual plants were sampled from 11 March 1983 through 12 March 1984 at 2-week intervals. Quadrats were placed at the edge of shrub canopies because annual plants are concentrated under *Larrea tridentata* canopies (Parker *et al.*, 1982). Twelve quadrats were placed at randomly selected points at the edge of shrub canopies in each treatment. We recorded the average diameter and the height of each plant in the quadrat. Plant sizes were transformed to dry biomass from allometric regression equations (Gutierrez, 1984; Gutierrez and Whitford, 1987). The data were analyzed by factorial ANOVAs and the proper error terms were used in order to reflect the split-plot design and the random arrangements of the plots. Treatment comparisons were done by LSD (Steel and Torrie, 1980).

Results

Total density and total aboveground biomass.—During the cold temperature months of November-May, soil water potential in the unwatered plots ranged between −0.5 MPa and −7.5 MPa at 5 cm and −1.0 MPa and −6.0 MPa at 15 cm. The 6-mm-per-week plots were generally −2.0 to −3.0 MPa wetter than the unwatered plots except for 10 days following a large rainfall in April (Table 1) when soils were at field capacity to 15

TABLE 1.—Natural precipitation (mm) on the study area during the germination and establishment periods of the herbaceous annual plants

1983						1984	
Jan	21.1	May	11.7	Sept	29.9	Jan	0
Feb.	13.9	June	3.8	Oct.	39.8	Feb	0
March	3.8	July	17.7	Nov.	26.9	March	6.4
April	22.6	Aug	39.3	Dec	0		

cm. The 25-mm-per-month application brought the upper 15 cm of soil to field capacity. In the cool months the 25 mm-plot soils dried to approximately −2.0 MPa between irrigations and in midsummer dried to −6 MPa. In summer the 6-mm plots dried to unwatered plot water potentials within 3-4 days after irrigation.

There were no significant differences in total mean densities of all annual plants in the different treatments and there were no water-nitrogen interaction effects on the total densities of all annuals ($F_{28, 167}$) = 1.34; $P > 0.10$). Total densities varied between three and 20 plants • m^{-1} except on 10 October 1983 when the density of annuals was higher in the 6 mm • $week^{-1}$ (36 • m^{-2}) than in the 25 mm • $month^{-1}$ (4 • m^{-2}) and unwatered plots (17 • m^{-2}) ($F(_{28, 167})$ = 1.55; $P < 0.05$). On the same date, densities of annuals were higher in the fertilized (82 • m^{-2} in 6 mm + N, 63 • m^{-2} in 0 mm + N and 31 • m^{-2} in 25 mm + N) than in the unfertilized plots ($F(_{14, 167})$ = 1.80; $P <$ 0.05). In October virtually all of the live plants on the plots were unidentifiable seedlings at the two cotyledon stage. These survived for a short period and the densities decreased by as much as 95% in November. The appearance of seedlings on the unwatered plots was associated with three natural large rainfall events. The first was at the end of August (24 mm), the second at the middle of September (17 mm) and the third at the beginning of October (21 mm) (Table 1).

Pooled biomass means were not significantly different for the water treatments (F $(_{2, 12})$ = 1.12; $P > 0.35$). Pooled biomass means were higher in the fertilized plots than in the unfertilized ones ($F(_{1, 12})$ = 10.21; $P < 0.01$) (Fig. 1). There were no water-nitrogen interaction effects on total annual plant biomass ($F(_{2, 12})$ = 1.16; $P > 0.30$).

Species responses.—The population densities of 12 of the 23 species recorded were sig-

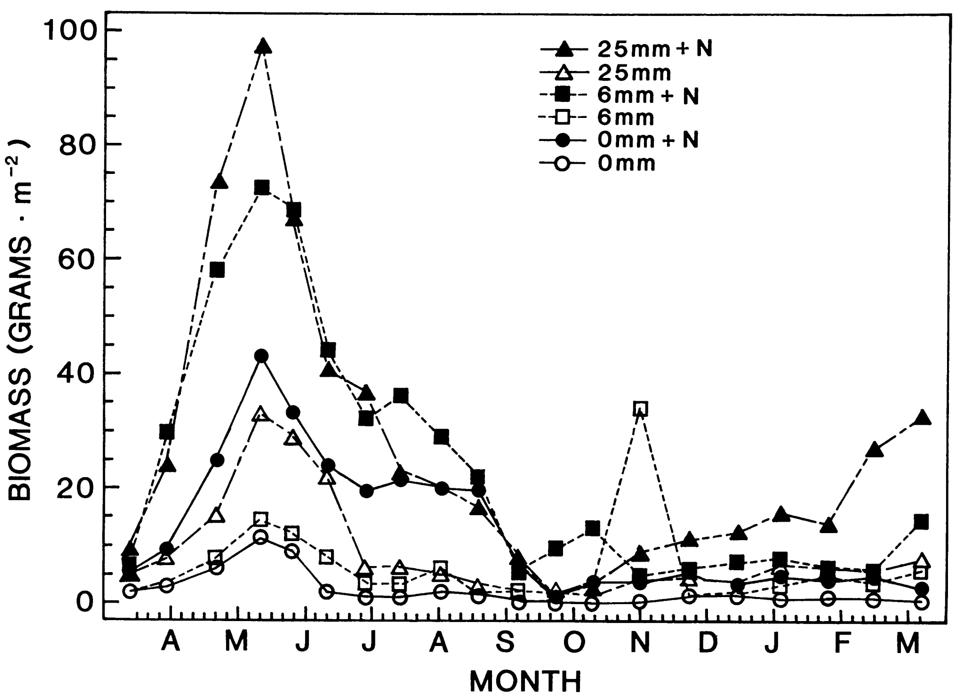

Fig. 1.—The effects of supplemental water applied at 6 mm • $week^{-1}$; 25 mm every 4th week with (+N) and without fertilization with NH_4NO_3 on the total biomass of annual plants on an area in the Chihuahuan Desert

nificantly higher in one or more of the treatments (Table 2). Two of the summer annuals, *Bouteloua aristidoides* and *Euphorbia serrula*, occurred only in fertilized plots. *Astragalus tephrodes* occurred in lower numbers in fertilized plots except in the 6 mm • week^{-1} plus N plots where nitrogen was leached from the surface soil layers. In general, species that responded numerically to water and nitrogen also had higher or lower biomass with the amendment, but that was not true in every species (Tables 2 and 3). More available nitrogen usually resulted in larger individual plants (Tables 2 and 3).

Community relationships. — The effects of water and nitrogen on the herbaceous annual plant communities were examined by the flexible cluster analysis strategy using densities of the species to compute chord-distances (Legendre and Legendre, 1983). This analysis provides a relative measure of similarity and groupings are considered different if separated by more than 1.0 units of chord distance. Two groups of related treatment plots were apparent (Fig. 2). The first group was the fertilized plots which were similar in the unwatered and 6 mm . week^{-1} plots. The second group was the unfertilized plots regardless of the watering treatment. (The 25 mm • month^{-1} plots were different from these two groups.)

DISCUSSION

Based on data in Kemp (1983), Chihuahuan Desert annual plants can be placed in one of three groups (*see* Tables 2 and 3): (1) winter-spring annuals that use the C_3 photosynthetic pathway, germinate in the autumn and grow as rosettes over the winter months, then bolt and set fruit between March and May; (2) spring annuals that use the C_3 photosynthetic pathway but germinate in late winter and may remain in the flower-fruiting stage throughout the summer if soil moisture is favorable, and (3) sum-

TABLE 2. — Peak biomass (g . m^{-2}) of annual plants on plots receiving 0 mm, 6 mm. wk^{-1} supplemental water and fertilized with nitrogen (+ N). Numbers in each row followed by the same letter are not significantly different (P < .05)

Spring annuals (C_3)	0mm	0mm + N	6mm	6mm + N	25mm	25mm + N
Astragalus tephrodes	0.1a	0.3a	2.5b	2.0b	4.5c	5.1c
Chaenactis stevioides	29.5a	81.81b	17.0a	150.0c	86.9b	116.7b
Crypthantha angustifolia	0.8a	4.26b	1.08a	9.7b	3.2b	16.1c
C. micrantha	<0.1a	<0.1a	<0.1a	0.8b	0.3b	0.8b
Descurainea pinnata	0.1a	2.2b	0.4a	4.0b	1.8b	3.2b
Dithyrea wislizenii	<0.1a	<0.1a	0.0a	<0.1a	0.4b	2.4c
Eriastrum diffusum	2.1a	1.7a	5.7b	13.0c	2.0b	1.8b
Lepidium lasiocarpum	7.4a	21.5b	9.9a	54.8c	4.6c	46.9c
Malacothrix fendleri	<0.1	0	0	0	0	0
Oenothera spp	0	0	<0.1	0	0	0
Spring-summer annuals (C_3)						
Baileya multiradiata	<.1a	<.1a	3.1b	3.6b	3.5b	0.5c
Eriogonum abertianum	0.2a	<.1b	0.4a	<.1b	<.1b	0.2a
E. rotundifolium	0	0.1	0	<.1	0	0
E. trichopes	0a	0.1b	1.4c	<.1b	4.1d	<.1a
Summer annuals (C_4)						
Bouteloua aristidoides	0	0	0	0.2	0	<.1
Euphorbia micromera	<.1	0	<.1	<.1	<.1	0
E. serrula	0	<.1	0	<.1	0	0
Mollugo cervenia	<.1a	0.4b	<.1a	<.1a	0.01a	0.06a

mer annuals which use the C_4 photosynthetic pathway, germinate following summer rainfall and mature in August through October.

The results of these studies support the hypothesis that nitrogen is an important factor limiting the biomass production of winter-spring annual herbs in the Chihuahuan Desert (Gutierrez and Whitford, 1987). In addition to affecting biomass production, nitrogen affected: (1) the species composition and relative importance of species in the annual herb communities; (2) length of life of some winter-spring and spring species, and (3) the diversity of annual herb communities. Williams and Bell (1981) found that adding 10 g N . m^{-2} as NH_4NO_3 increased productivity of Mojave Desert ephemerals up to 7x on a sandy soil but had no effect on annuals growing on alluvium. Their results show that annuals respond to N only on N-poor soils.

Our experiments did not support the hypothesis that rainfalls of 25 mm or greater are necessary to trigger growth of annual herbs (Beatley, 1974). Indeed, frequent low quantity water supplementation resulted in higher densities of winter-spring annuals, especially when applied to areas enriched by N fertilizer.

The high densities of seedlings recorded in October and differences in densities of seedlings among treatments raises some important questions. The data suggest that seed germination was affected by the nitrogen concentration in the surface soil layers. Although monthly water plus nitrogen had the lowest density of germinants, inorganic N in the surface layers would have been depleted by leaching. The monthly irrigation was applied 10 days prior to the October sampling. The enhancement of germination of annual herbs by inorganic nitrogen was reported by Young *et al.* (1981), who found that addition of 0.10 mm KNO_3 resulted in nearly double the number of germinants of miscellaneous forbs in comparison to water only. The data of Young *et al.* (1981) and data from this study suggest that inorganic nitrogen enhances germination by some un-

TABLE 3.—Peak density (number . m^{-2}) of annual plants on plots receiving 0 mm, 6 mm. wk^{-1} and 25 mm. mo^{-1} supplemental water and fertilized with nitrogen (+ N). Numbers in each row followed by the same letter are not significantly different ($P < .05$)

Spring annuals (C_3)	0mm	0mm + N	6mm	6mm + N	25mm	25mm + N
Astragalus tephrodes	5.2a	2.6c	2.6c	4.0b	6.6a	3.6b
Chaenactis stevioides	5.9a	5.9a	4.9a	6.2a	7.9a	6.4a
Crypthantha angustifolia	3.6a	4.5a	5.6b	6.2b	6.2b	9.2c
C. micrantha	0.9a	0.8a	2.1b	2.3b	4.1c	3.5c
Descurainea pinnata	2.9a	2.8a	5.7b	3.3a	6.4b	4.2ab
Dithyrea wislizenii	0.2a	0.7a	0.0	0.4ab	0.2a	0.5b
Eriastrum diffusum	10.4a	6.4b	3.0c	5.5bc	2.4c	1.4c
Lepidium lasiocarpum	7.4a	7.6a	10.6b	9.9b	6.9a	8.7ab
Malacothrix fendleri	0.2	0	0	0	0	0
Oenothera spp	0	0	0.2	0.2	0	0.2
Spring-summer annuals (C_3)						
Baileya multiradiata	0.9a	0.2a	5.8b	3.1b	2.9b	0.9a
Eriogonum abertianum	3.1a	0.6b	0.9b	0.3b	0.6b	0.2b
E. rotundifolium	0	0.4	0	0.3	0	0
E. trichopes	1.0a	0.9a	1.6a	0.3b	0.6a	0.2b
Summer annuals (C_4)						
Bouteloua aristidoides	0	0	0	0.3	0	0.2
Euphorbia micromera	0.2	0	0.5	0.5	0.5	0
E. serrula	0	0.4	0	0.2	0	0
Mollugo cervenia	6.6a	6.4a	4.0b	2.8b	2.6b	0.9c

known mechanism. The reduction in densities of the germinants by the November sampling probably resulted from self-thinning. Watering increased the density and biomass of the relatively nitrogen-independent species *Astragalus tephrodes* and *Bailey multiradiata*. *Astragalus tephrodes* is a legume with nitrogen-fixing *Rhizobium* nodules in its root system (pers. observ.), and water addition probably increased bacterium-nodule formation (Lauenroth and Dodd, 1979). Consequently, nitrogen fertilization may not affect the abundance of this species. Similar effects have been detected in shortgrass prairie legumes where nitrogen fertilization had an inhibitory effect on nodule formation (Lauenroth and Dodd, 1979). *Bailey multiradiata* have mycorrhizae associated with its roots (J. Zak, pers. comm.) and fertilization decreased density of this species but did not affect *B. multiradiata* biomass.

Watering of 25 mm in a single event had a greater effect on *Astragalus tephrodes* biomass than the weekly watering of 6 mm as predicted by Beatley (1974). Density and biomass of *Bailey multiradiata*, however, was significantly higher in the weekly watered plots. Watering increased the number of plants of *Crypthantha micrantha* and *Descurainea pinnata* but did not affect their biomasses. These results reveal the importance of studying both density and biomass of the species simultaneously to understand what component is being affected by the treatments.

Lepidium lasiocarpum germinants accumulated biomass significantly faster with the smaller but more frequent water inputs (6 mm . week^{-1}) than in the 25 mm . month^{-1} irrigations. Apparently the frequency and amount of water required by *L. lasiocarpum* varies as the plant develops. Decreased density of *Eriastrum diffusum* in the watered plots suggests that *E. diffusum* may be a poor competitor with other species.

Nitrogen fertilization had a greater effect on plant biomass than on plant density. Biomass of several species increased with the nitrogen fertilization; however, densities of *Eriastrum diffusum*, *Eriogonum abertianum* and *E. trichopes* were lower in the fertilized plots. These species germinate late (April and May) and therefore they would be at a competitive disadvantage with respect to those species germinating early (*e.g.*, *Chaenactis stevioides* and *Lepidium lasiocarpum*). Nitrogen fertilization provides conditions for fast growth of plants germinating early and under those conditions established plants could deplete the

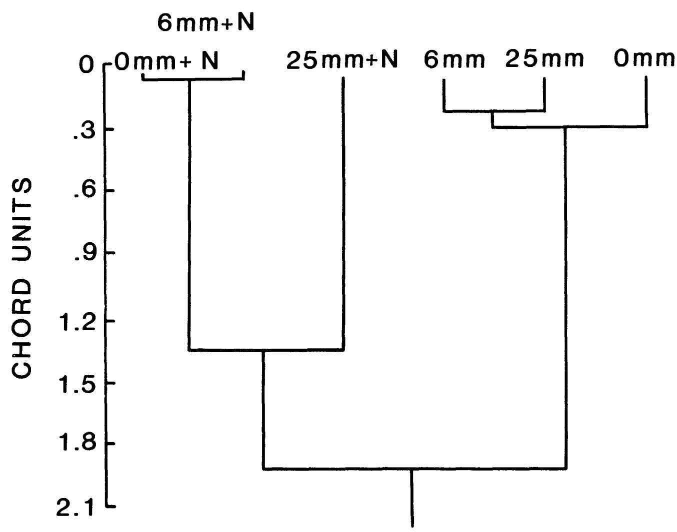

Fig. 2.—The relative similarity among assemblages of Chihuahuan Desert annual plants as measured by flexible cluster analysis using densities of species to compute chord distances

soil nitrogen supply affecting the establishment of the species germinating later (*see* Rathcke and Lacey, 1985, and citations therein).

Diversity was higher in the weekly watered-unfertilized plots than in the monthly watered plots, but fertilization of the weekly watered plots decreased species diversity. These results suggest that when extra resources are available some species respond by increasing size or density and may, therefore, out compete other species (Tilman, 1982). Another effect of nitrogen fertilization was to change species dominance in the spring annual assemblages. *Lipidium lasiocarpum*, which was a subordinate species in the unfertilized plots, shared dominance with *Chaenactis stevioides* in the fertilized plots. Changes in species dominance in response to nitrogen fertilization has been reported for grasslands (Tilman, 1984). Since differences and similarities among experimental plots were tied to nitrogen fertilization, nitrogen appears to be the primary factor affecting species composition.

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Literature Cited

BEATLEY, J.C. 1974. Phenological events and their environmental triggers in Mojave Desert ecosystems. *Ecology*, **55**:858-863.

GUTIERREZ, J.R. 1984. Ephermeral plant responses to termites, water and nitrogen in a Chihuahuan Desert. Ph.D. Dissertation, New Mexico State University, Las Cruces. 109 p.

——— AND W.G. WHITFORD. 1987. Responses of Chihuahuan desert herbaceous annuals to rainfall augmentation. *J. Arid Environ.*, **12**:127-139.

HOUGHTON, F.E. 1972. Climatic guide. New Mexico State University, Las Cruces, 1851-1971. *N. M. Agric. Exp. Stn. Res. Rep.*, **230**:1-20.

KEMP, P.R. 1983. Phenological patterns of Chihuahuan Desert plants in relation to the timing of water availability. *J. Ecol.*, **71**:427-436.

LAUENROTH, W.K. AND J.L. DODD. 1979. Response of native grassland legumes to water and nitrogen treatments. *J. Range Manage.*, **32**:292-294.

LEGENDRE, L. AND P. LEGENDRE. 1983. Numerical ecology. Elsevier Scientific Publishing Co., Amsterdam. 419 p.

PARKER, L.W., H.G. FOWLER, G. ETTERSHANK AND W.G. WHITFORD. 1982. The effects of subterranean termite removal on desert soil nitrogen and ephemeral flora. *J. Arid Environ.*, **5**:53-59.

———, P.F. SANTOS, J. PHILLIPS AND W.G. WHITFORD. 1984. Carbon and nitrogen dynamics during the decomposition of litter and roots of a Chihuahuan Desert annual *Lepidium lasiocarpum*. *Ecol. Monogr.*, **53**:339-360.

RATHCKE, B. AND E.P. LACEY. 1985. Phenological patterns of terrestrial plants. *Annu. Rev. Ecol. Syst.*, **16**:179-214.

SALA, O.E. AND W.K. LAUENROTH. 1981. Small rainfall events: an ecological role in semiarid regions. *Oecologia*, **53**:301-304.

SKUJINS, J.J. 1981. Nitrogen cycling in arid ecosystems, p. 477-491. *In*: F.E. Clark and T. Roswall (eds.). Terrestrial nitrogen cycles. Ecological Bulletin, Stockholm. 554 p.

STEEL, R.G.D. AND J.H. TORRIE. 1980. Principles and procedures of statistics. McGraw-Hill, New York. 633 p.

TILMAN, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, New Jersey. 296 p.

TILMAN, G.D. 1984. Plant dominance along an experimental nutrient gradient. *Ecology*, **65**:1445-1453.

WEST, N.E. AND J.J. SKUJINS. 1978. Nitrogen in desert ecosystems. Dowden, Hutchinson & Ross, Stroudsburg, Pa. 307 p.

WILLIAMS, R.B. AND K.L. BELL. 1981. Nitrogen allocation in Mojave desert winter annuals. *Oecologia,* **48**:145-150.

YOUNG, J.A., R.A. EVANS, C.A. RAGUSE AND J.R. LARSON. 1981. Germinable seeds and periodicity of germination in annual grasslands. *Hilgardia*, **49**:1-37.

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