Journal of Arid Environments 104 (2014) 96–105

Contents lists available at ScienceDirect

Journal of Arid Environments

journal homepage: www.elsevier.com/locate/jaridenv

Altered nitrogen and precipitation along urban gradients affect harvester ants and seed sources

B.D. Wissinger[a,*], S.D. Eigenbrode[b], J.D. Marshall[a], J.D. Hoines[c], B.A. Newingham[a]

[a] Department of Forest, Rangeland, and Fire Sciences, University of Idaho, Moscow, ID 83844-1143, USA
[b] Department of Plant, Soil and Entomological Sciences, University of Idaho, Moscow, ID 83844-2339, USA
[c] U.S. Department of the Interior, National Park Service, Joshua Tree National Park, Twentynine Palms, CA 92277, USA

ARTICLE INFO

Article history:
Received 4 July 2013
Received in revised form
10 January 2014
Accepted 11 February 2014
Available online 13 March 2014

Keywords:
Atmospheric nitrogen deposition
Carbon dioxide
Larrea tridentata
Messor pergandei
Precipitation

ABSTRACT

We investigated the effects of nitrogen deposition and precipitation on *Messor pergandei* (Mayr) harvester ants and plants to identify alterations in the desert food web in California. We measured ant colony attributes and shrub fruit densities, as well as nitrogen and carbon concentrations and stable isotopes, at 18 sites along a nitrogen deposition gradient. Ant nest density increased from low to high deposition sites; however, ant nest mound size and the density of abandoned nests decreased as deposition increased. Nest mound size was positively correlated with the size and age of the colony; therefore, these results suggest that colonization has been more frequent with increased inter-colony competition in areas of high deposition. Nitrogen and carbon isotope values of perennial plant leaves and seeds, annual plant seeds, and ants were significantly enriched in the heavy isotopes from low to high nitrogen deposition regions, indicating the possibility of plants assimilating different sources of both elements, including anthropogenically-produced compounds. Plant carbon isotope discrimination also differed with the decrease in precipitation across the gradient. Considering that deserts are limited by both nitrogen and precipitation, our results suggest that altered nitrogen inputs in conjunction with precipitation may result in cascading effects through trophic levels and drive arid ecosystem change.

1. Introduction

Global changes, including atmospheric nitrogen deposition and altered precipitation regimes, are driving novel ecosystem responses. Nitrogen deposition can affect soil microbial processes and plant available nitrogen producing alterations in ecosystem structure and function (Fenn et al., 2003a; Rao et al., 2009; Sirulnik et al., 2007; Vourlitis et al., 2007). A synthesis by Bobbink et al. (2010) found that nitrogen is more critical in determining community composition than previously realized. These alterations typically result in increases in nitrogen availability that can cause weedy plant invasions in desert systems, altering fire regimes and plant community composition (D'Antonio and Vitousek, 1992; Evans et al., 2001; Schwinning et al., 2005). Most current studies focus on the effects of nitrogen deposition on one trophic level or taxonomic group; few studies examine the cascading effects of nitrogen deposition across trophic levels.

The arid western United States experiences primarily dry nitrogen deposition, which has dramatically increased over the last several decades from sources such as motor vehicle exhaust, power plant emissions, industrial emissions, agricultural field fertilization, and feedlots (Fenn et al., 2003a). For example, Los Angeles, California, USA, and nearby population centres create substantial amounts of pollution, including nitrogenous compounds from motor vehicle exhaust, each year through fossil fuel combustion (Fenn et al., 2003b; Allen et al., 2009). The nitrogen is carried across southern California and falls out as winds move east, creating a nitrogen deposition gradient. This nitrogen deposition gradient extends about 150 km across the Coachella Valley and Joshua Tree National Park, providing a unique opportunity to examine the ecological effects of such a gradient. Rao et al. (2009) and Allen et al. (2009) detailed changes in soil processes and annual plant communities following large pulses of nitrogen fertilizer within this gradient; however, it is not known whether these changes have influenced higher trophic levels.

* Corresponding author. College of Natural Resources, University of Idaho, PO Box 441133, Moscow, ID 83844-1143, USA. Tel.: +1 208 885 6538; fax: +1 208 885 5190.
E-mail address: benwissinger@gmail.com (B.D. Wissinger).

http://dx.doi.org/10.1016/j.jaridenv.2014.02.001

The effects of an altered hydrologic and nitrogen cycle in the Mojave and Colorado Desert systems are complex and not well known. If declines in rainfall and soil moisture reduce nitrogen availability, plant populations and the animals that depend on them could be negatively impacted. Conversely, increases in nitrogen deposition could mitigate reductions in microbially-produced nitrogen in low precipitation environments (Vourlitis et al., 2007).

Little is known about seed production and subsequent granivory under elevated nitrogen (Throop and Lerdau, 2004). Higher nitrogen levels typically result in increased plant biomass production and higher tissue nitrogen concentrations, which can regulate trophic structure (Cebrian et al., 2009). Throop and Lerdau (2004) found higher growth or consumption rates in leaf-feeding insects with increased nitrogen in the majority of twenty studies reviewed. Considering that nitrogen is highly limiting for most consumers, plants producing more seed or seed with higher nitrogen concentrations could cause an increase in populations of granivores, including harvester ants (Throop and Lerdau, 2004). Granivory and seed movement can deplete plant populations and/or shift species composition (MacMahon et al., 2000; White and Robertson, 2010). Thus, how plants and granivores react to nitrogen deposition is critical as the effects of increased nitrogen on plant and seed characteristics could have large consequences for desert ecosystems (Kelrick et al., 1986).

Harvester ants, birds, and rodents move, store, and consume mass quantities of seed (MacMahon et al., 2000; White and Robertson, 2010). The harvester ant, *Messor pergandei (Mayr)*, is a ubiquitous and important granivore in the deserts of southern California and is co-dominant with *Pogonomyrmex* species (Went et al., 1972). Seeds from annual forbs and grasses are typically harvested, but perennial shrub and grass seeds are also collected (Went et al., 1972; Wissinger, *personal observation*). Seed refuse, flowers, stems, and other debris are brought from inside the nest and deposited around the nest entrance, creating large mounds (Went et al., 1972). The size of these mounds is correlated with the size and age of the ant colony inhabiting the nest (Gordon, 1984; Wagner and Gordon, 1997).

Considering the significance of harvester ants in desert ecosystems, it is essential to understand the effects of altered nitrogen and precipitation on this key species and its food sources. We investigated how atmospheric nitrogen deposition and precipitation affected multiple trophic levels, including plants, seeds, and seed-harvesting ants across a nitrogen deposition and precipitation gradient in the Coachella Valley and Joshua Tree National Park, California. The use of stable isotopes enabled us to track nitrogen and carbon assimilation by the organism in successive trophic levels. Our study asked: 1) Are harvester ant nest densities greater in areas with higher nitrogen deposition and precipitation? 2) Does ant nest size change in areas with higher nitrogen deposition and precipitation? 3) Is seed production increased with higher nitrogen deposition and precipitation? 4) Do areas of higher nitrogen deposition and precipitation alter $\delta^{13}C$ and $\delta^{15}N$ and percent carbon and nitrogen across trophic levels?

2. Materials and methods

2.1. Site selection and description

We examined 18 sites across a nitrogen (N) deposition gradient located in the Colorado and Mojave deserts, which stretched from the west end of the Coachella Valley to the east side of Joshua Tree National Park (Figure A1, Table A1). Nine sites were within the park boundaries, while another nine sites were situated among urban areas between Interstate 10 and the park. We selected sites based on the presence of *M. pergandei* ants and their inclusion within an established atmospheric nitrogen deposition gradient (Allen et al., 2009; Rao et al., 2009). For this study, nitrogen deposition values were obtained from a Models-3/Community Multiscale Air Quality (CMAQ) model (Fenn et al., 2003b; Tonnesen et al., 2007) and HNO_3 atmospheric concentrations from 2010 to 2011 sampling efforts (Bell, 2012).

Nitrogen deposition gradients are often accompanied by other abiotic gradients (Hall et al., 2011; Rao and Allen, 2010). In order to account for other possible gradients, we also determined annual precipitation, atmospheric CO_2 concentrations, and soil nitrogen across our study sites. Annual precipitation values from 2001 to 2011 for each site were obtained from the PRISM model and were averaged (PRISM Climate Group, 2004, Fig. 2). Atmospheric CO_2 concentrations were of interest because *Larrea tridentata* may increase nitrogen uptake under high CO_2 conditions (Jin and Evans, 2010). Additionally, elevated atmospheric CO_2 concentrations affect water use efficiency in many plants (Farquhar et al., 1989). Thus, atmospheric CO_2 concentrations and ^{13}C values for background atmospheric CO_2 were measured by taking three air samples from each of six representative sites (two sites each from the west end, middle, and east end) across the gradient. Air was collected in vials during the early afternoon and stored until analysis on a Gasbench II (Thermo Finnigan) coupled with a continuous-flow isotope-ratioing mass spectrometer (Thermo Finnigan DELTA plus) at the University of Idaho Stable Isotopes Laboratory. To determine soil nitrogen at each site, we collected ten soil samples five centimeters deep and thoroughly mixed them in the field. At the University of Idaho, soil nitrogen in the forms of nitrate.

(NO_3^-) and ammonium (NH_4^+) was extracted using potassium chloride (KCl). The resulting solutions were evaluated by flow injection analysis at the Soil and Plant Analysis Laboratory, Brigham Young University, Provo, Utah.

The sites were located in *L. tridentata* (DC.) Coville (evergreen shrub)/*Ambrosia dumosa* (A. Gray) (drought-deciduous shrub) vegetation communities. Other co-occurring native shrubs included *Encelia farinosa* (A. Gray ex Torr.) and *Hymenoclea salsola* (A. Gray). Common native annual forbs such as *Cryptantha*, *Corzanthe*, *Eriodium*, and many *Aster* species were present with non-native grasses (*Schismus* spp. and *Bromus rubens* L.) and non-native forbs (e.g., *Brassica tournefortii* Gouan). Soil texture at each site was either loamy sand or sand. Sites were located in sandy washes, basins, or bajadas, and ranged from approximately 90–715 m above mean sea level (Table A1). Sites are described as the distance from Cabazon, California, USA, where sites closest to Cabazon (west side of study area) have the highest nitrogen deposition and annual precipitation; sites furthest from Cabazon (east side of study area) have the lowest nitrogen deposition and annual precipitation.

2.2. Field measurements

At each site across the gradient, plant and harvester ant measurements were taken on two perpendicular transects intersecting at their midpoints to form crosses. We established five crosses per site and the center point of each cross was separated by 300 m. Each segment of the cross was 100 m long by 4 m wide, which allowed us to survey 1600 m^2. Thus, at each site we surveyed a total of 8000 m^2.

For three of the five crosses at each site, we measured shrub density and counted fruits and seeds. All *A. dumosa* and *L. tridentata* shrubs were counted within the 1600 m^2 sample area. Fruit and seed counts were obtained from 20 individual shrubs of each species in each cross from shrubs nearest the centerline at 20, 40,