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Phytophagous insects enhance nitrogen flux in a desert creosotebush community

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Summary. We tested the hypothesis that herbivorous insects on desert shrubs contribute to short-term nitrogen cycling, and increase rates of nitrogen flux from nutrient rich plants. Creosotebush (*Larrea tridentata*) shrubs were treated with different combinations of fertilizer and water augmentations, resulting in different levels of foliage production and foliar nitrogen contents. Foliage arthropod populations, and nitrogen in canopy dry throughfall, wet throughfall and stemflow were measured to assess nitrogen flux rates relative to arthropod abundances on manipulated and unmanipulated shrubs over a one-month period during peak productivity. Numbers and biomass of foliage arthropods were significantly higher on fertilized shrubs. Sap-sucking phytophagous insects accounted for the greatest numbers of foliage arthropods, but leaf-chewing phytophagous insects represented the greatest biomass of foliage arthropods. Measured amounts of bulk frass (from leaf-chewing insects) were not significantly different among the various treatments. Amounts of nitrogen from dry and wet throughfall and stemflow were significantly greater under fertilized shrubs due to fine frass input from sap-sucking insects. Increased numbers and biomass of phytophagous insects on fertilized shrubs increased canopy to soil nitrogen flux due to increased levels of herbivory and excrement. Nitrogen excreted by foliage arthropods accounted for about 20% of the total one month canopy to soil nitrogen flux, while leaf litter accounted for about 80%.

Key words: Desert shrubs – *Larrea tridentata* – Nitrogen cycling – Insects

Consumers may influence ecosystem nutrient cycling by increasing rates of nutrient fluxes (Chew 1974; Mattson and Addy 1975; Petrusewicz and Grodzinski 1975; Springett 1978; Kitchell et al. 1979). Total amounts of nutrients flowing through consumer trophic levels are small relative to amounts flowing through producer and decomposer levels, yet the rates at which nutrients are transferred between producers and decomposers may be increased by consumers. Herbivores consume primary production, skimming off nutrients and returning some of them to the soil, and subsequently back to producers at rates faster than the nutrients would otherwise flow through the processes of senescence, litter fall, and decomposition. Herbivores affect nutrient cycling rates in other ways, by stimulating plant growth and nutrient uptake (McNaughton 1985), increasing litter production (Carlisle et al. 1966a, b; Risley 1986), increasing the nutrient content of litter (Owen 1978), enhancing the rates of litter decomposition (Owen and Wiegert 1976), and by increasing nutrient leaching from foliage (Parker 1983).

Theory behind the concept that consumers regulate rates of nutrient cycling has been developed primarily from forest (Reichle et al. 1973; Mattson and Addy 1975; Springett 1978; Schowalter 1981) and grassland (McNaughton 1979, 1985) ecosystems. Most studies testing various hypotheses concerning consumer regulation of nutrient cycling have been conducted in forest ecosystems, and some have yielded results indicating that consumers increase nutrient flux rates (Carlisle et al. 1966a; Schowalter et al. 1981; Swank et al. 1981; Fogal and Slansky 1985; Hollinger 1986), while others have found little or no consumer effect on nutrient fluxes (Ohmart et al. 1983; Seastedt et al. 1983).

Nitrogen cycling in desert ecosystems differs from mesic systems due to the spatially and temporally variable supply of nitrogen in deserts (West and Skujins 1978; West 1981), and the magnitude and duration of productivity pulses when they occur (Noy-Meir 1973; Hadley and Szarek 1981). In desert shrub ecosystems, accumulations of nitrogen in soil and biomass are lower than in forests or grasslands on a per hectare basis (Skujins 1981), yet nitrogen accumulations are quite high around shrubs which typically cover only a small percentage of the total landscape (Charley 1972; Crawford and Gosz 1982). Since the majority of internal nitrogen cycling in desert shrub ecosystems is centered around shrubs (Skujins 1981), insect herbivores that live on those shrubs may influence rates of nitrogen fluxes between desert plants and soils.

Our previous work on foliage arthropods of creosotebush (*Larrea tridentata*) demonstrated that levels of foliage production, foliar nitrogen contents, and densities of phytophagous insects all increased in response to nitrogen fertilization of plants (Lightfoot and Whitford 1987). The present study was conducted to determine if foliage arthropods produce a significant short-term canopy to soil nitrogen flux from creosotebush shrubs, and if increased densities of phytophagous insects on high nutrient fertilized shrubs significantly increase amounts of nitrogen throughfall to the soil surface via increased feeding and excretion. In accordance with current theory (e.g. Mattson and Addy 1975; Kitchell et al. 1979), we predicted that insect populations on creosotebush shrubs should increase rates of nutrient

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flux from shrubs with increased nutrient contents and productivity. For a stress-tolerant evergreen shrub such as creosotebush (Grime 1977; Reynolds 1986), short-term increases in nitrogen cycling rates could facilitate multiple pulses of productivity following temporally separated periods of rainfall within a single growing season.

Methods

Study site and experimental design

The study site was located in the northern Chihuahuan Desert at the Jornada Long-Term Ecological Research site near Las Cruces, New Mexico. The experimental design, plots, and creosotebush shrubs were the same as in our previous study (Lightfoot and Whitford 1987). We employed a split-plot factorial experimental design utilizing nine 5×10 m plots receiving supplemental water and nitrogen. Three simulated rainfall treatments were randomly assigned to the plots, consisting of three plots as controls (no watering), three plots receiving 6 mm of water once each week, and three plots each receiving 25 mm of water once every four weeks. Simulated rainfall was applied through a series of fixed sprinklers that were positioned above the shrub canopies. Water treatments were begun in the summer of 1981. One half of each of the plots was treated with the equivalent of 100 kg/ha of ammonium nitrate fertilizer by one application in February, 1983.

Field sampling for this investigation was conducted over a 4 week period from May 14 to June 12, 1984. Productivity in desert systems typically occurs in pulses over short periods of time (Noy-Meir 1973; Hadley and Szarek 1981), during which consumer effects on nutrient fluxes are likely to be most prevalent. Therefore, we sampled over a time period when creosotebush productivity and foliage arthropod populations tend to be greatest in the northern Chihuahuan Desert.

Five similar sized shrubs in each of the half-plots were tagged and measured for plant responses to the treatments. Branch growth and foliar nitrogen contents were measured in 1983 (Lightfoot and Whitford 1987), but not in 1984. In 1983 we found that foliage production and foliar nitrogen contents were significantly higher in shrubs that were fertilized. A weak fertilizer-water interaction effect was evident, but water alone had no effect on creosotebush foliage production or foliar nitrogen contents. Foliage arthropods, dry and wet throughfall, and stemflow were sampled from those same 90 shrubs in the present study, and we assumed that the treatment effects on shrubs that we observed in 1983 were similar in 1984.

Foliage arthropods

Foliage arthropods were sampled from one branch on each of the tagged shrubs. Each shrub was sampled twice during the four week study period, once after two weeks (May 25) and once at the end of four weeks (June 13). Similar sized branches were randomly sampled from all shrubs, each was placed into a 40 cm diameter insect sweep net, and shaken to dislodge arthropods from the branch into the net. Shrubs were sampled at sunrise when arthropod activity was low. The net contents from each branch were then emptied into zip-lock plastic storage bags and were sorted in the lab. Arthropods were counted and categorized to taxa and trophic group. Ten individuals of all common taxa were fresh weighed for trophic group biomass estimates.

Dry throughfall

Dry throughfall (arthropod frass and plant litter) from the shrub canopies was collected in wide mouth pint (0.47 l) Mason jars placed on the ground under the canopy of each tagged shrub. A jar was also placed in an open inter-shrub space near the middle of each of the nine plots to collect atmospheric dry-fall. Each collecting jar contained two filter paper cones folded from 15 cm Whatman no 1 qualitative filter paper. One filter paper cone was placed apex down, in the bottom of each jar to catch and contain solid material falling into the jar. Another cone was taped basally to the mouth of each jar, apically directed downward, with the tip cut out to allow material to fall into the bottom cone, but preventing the wind from blowing material out of the jar. Dry throughfall jars were sampled twice during the four week period, at the end of two weeks (May 28) and at the end of the four weeks (June 11). Jars were left open for two weeks at a time, but closed briefly during simulated and natural rainfall events.

Small amounts of accumulated plant litter were removed, and the remaining contents were oven dried (50° C) and weighed. Large particles of frass (>0.5 mm, large enough to be picked up with watchmaker forceps) were weighed separately. We refer to these large particles of frass as bulk frass. Much of the frass was in the form of fine particles (<0.5 mm) too small to be handled and weighed separately from the filter paper. Variation in filter paper weight alone was too great to measure fine frass as a component of total filter paper weight. Therefore, we could not adequately measure total frass weight, and bulk frass weight does not represent total frass weight.

The filter paper and bulk and fine frass from each jar were ground together and analyzed for total nitrogen by Kjeldahl digestion and colorametric measurement by autoanalizer. Measures of mean total nitrogen from control jars in the open inter-shrub spaces were subtracted from the total nitrogen measurements of each jar placed under shrubs to correct for nitrogen already present in the filter paper and additional nitrogen from atmospheric deposition. Accumulations of nitrogen in dry-fall control jars averaged about 78.0 mg/m for the one-month period, which was considerably higher than the 15.6 mg/m of nitrogen that accumulated over the same time in an atmospheric dry-fall collector (Aerochem Metrics, model 301 automatic sensing wet/dry precipitation collector) located at the study site. Jars placed on the ground contained more wind blown organic material than the dry-fall collector, and jars occasionally trapped flying insects such as flies (Diptera), bees and wasps (Hymenoptera), which were included in nitrogen analyses, and probably elevated levels of nitrogen in those samples.

Creosotebush leaf litter was not collected directly on the study plots, but was sampled from 10 nearby unfertilized, unwatered shrubs. Screen litter collectors were placed under the entire canopies of those shrubs and accumulated litter was sampled once every 4 weeks. Data from litter that accumulated from May 1 to June 1 were used for this study. The accumulated litter from each shrub was dry weighed, and then analyzed for total nitrogen by Kjel-