Nitrogen Allocation in Mojave Desert Winter Annuals

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Summary. Nitrogen contents and allocation were examined in winter annuals at two Mojave Desert sites near Boulder City, Nevada. Application of 10 g N m⁻² as NH₄NO₃ increased production 0- to 7-fold in species growing on a sandy soil (an Entisol) but fertilizer had no effect on plants on an alluvium (an Aridisol). Tissue nitrogen comprised 0.09-3.5% of dry weight with the lowest concentrations found in vegetative organs of nitrogen-responsive plants. During development, nitrogen-poor species showed only minor changes in nitrogen concentration and allocation compared with more nitrogen-rich species. Maximum reproductive nitrogen allocation varied among species from 43 to 67%, while reproductive biomass allocation was 31 to 51%. Fertilizer increased reproductive biomass allocation by 7 to 16%, reproductive nitrogen concentrations by 120 to 260%, and leaf and root nitrogen concentrations by 200 to 615% in nitrogen-deficient plants. Nitrogen-poor plants appear to allocate nitrogen to reproduction at the expense of vegetative organs throughout the life cycle.

Introduction

Considerable attention has recently centered on the role of nitrogen as a limiting factor to the growth of desert plants. Application of nitrogen fertilizer has little effect on shrub production, but it greatly increases production of annual herbs in the northern Mojave Desert (Wallace et al. 1978). Winter annual growth is so highly dependent upon nutrient availability that relatively nitrogen-rich "fertile islands" beneath shrubs support much larger plants with higher production efficiency than the nitrogen-poor soil in open areas (Mott and McComb 1974; Halvorson and Patton 1975; Romney et al. 1978; Patton 1978).

A comparison of tissue nitrogen concentrations suggests that Mojave Desert annuals generally have considerably lower levels (0.43-2.07% of dry weight) than perennial shrubs (1.12-5.54%) (Wallace et al. 1978). Perennials appear to achieve higher levels of tissue nitrogen by exploiting a large soil volume and by highly effective internal conservation of nitrogen (Wallace et al 1978). Both of these mechanisms are likely to be unique to the perennial life cycle. Mojave winter annuals appear to have little organ replacement during their short lives, minimizing internal recycling; and their small root systems are often crowded in the upper 10 to 20 cm of the soil (Cannon 1911; Bell et al. 1979), leaving only the resources of a small soil mass available to each individual.

Annuals allocate a high proportion of their resources to reproduction; and if nitrogen is to be conserved from generation to generation, it must be at the expense of vegetative nitrogen. Reproductive biomass allocation in Mojave Desert winter annuals ranges from 16 to 50% (Bell et al. 1979). In mesophytic annuals, both native and cultivated, reproduction appears more costly in terms of nitrogen than in total biomass (Pate and Flinn 1973; Andel and Vera 1977), although loss of carbon through respiration is probably partially responsible for these results (Spiertz 1977). The necessity for conserving nitrogen between generations ought to be great for nitrogen-limited desert annuals. At the same time, the short growing season in many years makes a high rate of photosynthesis beneficial, and photosynthetic capacity is often closely linked to leaf nitrogen content. Thus, reproductive and photosynthetic organs may compete for the small pool of nitrogen available within the plant.

The experiments reported here sought to accomplish the following for Mojave Desert winter annuals: 1) determine whether test plants were responsive to nitrogen fertilizer and, therefore, nitrogen-limited; 2) determine tissue nitrogen levels in various plant organs as they developed to assess the extent of nitrogen concentration in reproductive structures during fruit maturation; 3) compare the nitrogen and biomass costs of various tissues by examination of nitrogen and biomass allocation during the growth of selected species; and 4) examine how nitrogen-impoverished plants invest supplemental nitrogen as a clue to what functions suffer most under suboptimal conditions. A variety of species were studied at sites on two different soils near Boulder City, Nevada. In an effort to minimize the variation between plots, and to increase the probability of studying plants having nitrogen deficiencies, all studies examined plants growing between shrubs.

Study Sites

Two sites were selected in typical low-elevation Mojave Desert plant communities dominated by Larrea tridentata and Ambrosia dumosa. One area was located in a deep sand soil (an Entisol) at about 680 m elevation, and test plots were scattered throughout an area 1.5 to 3.0 km southwest of Boulder City, Nevada. The other site lay on an eroding alluvium on a gentle northwest-facing slope at 730 m elevation, 6.5 km west of Boulder City. The Aridisol at the alluvium site

1 Nomenclature follows that of Munz (1974)
had a calcium carbonate hardpan at 1 to 2 m depth and a surface pavement of small stones.

Both sites supported mixed stands of winter annuals. No single annual species grew at both sites. Dominant species varied among the three winters of the study. In the sandy soil, the most common species included Schismus arabicus in all years; Genusidea deloides, Baileya pentradia, and Astragalus sabulonum in 1976-1977; Chaenac-
tis fremontii, Cryptantha pterocarya and C. angustifolia in 1977-1978; and Eriogonum trichopes and Eriogonum triphylops in 1978-1979. On the alluvium, dominant species in the areas between shrubs included Plantago insularis and Chaenacitis carphoclinia in all three years, 1976–

Methods

Two sets of fertilizer response studies were conducted. Response of annuals to nitrogen as \( \text{NH}_4\text{NO}_3 \) was examined at both the sand and alluvium sites. Square 1 m² plots were fertilized during heavy rains 19-20 November 1978. The fertilizer was applied as a saturated solution. Treatments consisted of five plots each of 0, 5, 10, 20 and 30 g N m -2 at both sites; 1 g m -2 plots were established only on the alluvium. Plots were placed between shrubs and treatments assigned randomly. All annual growth, including roots, was harvested on 5 to 10 May 1979 when all species were approaching seed dispersal. Developmental shifts in nitrogen allocation, two species, Schismus arabicus and Chaenacitis carphoclinia which was beginning seed dispersal. Whole plots were harvested on the outwash slope, and 25 × 25 cm plots in the more productive sandy soil community.

A second set of experiments in the sandy soil investigated both responses to nitrogen and phosphorus and the allocation of supplemental nitrogen in selected species. For these tests, 16 circular plots, 1 m in diameter, were placed randomly in areas between shrubs on the sandy soil. Four of these plots were used for each of four treatments: unfertilized controls; nitrogen-fertilized with 10 g N as \( \text{NH}_4\text{NO}_3 \) m -2; phosphorus-fertilized with 5 g P m -2 as superphosphate; and combined nitrogen and phosphate at 10 g N and 5 g P m -2. Plots were watered, fertilized, and watered again on 18 February 1978, approximately one month after germination of annuals. Plots were harvested on 22 April 1978.

Tissue nitrogen concentrations were determined using a modified micro-Kjeldahl technique (Mitchell 1972). Tissues of like kind from several plants were pooled, when necessary, to provide adequate quantities for analysis. Five to eight replicates were run for each sample. Allocation studies were conducted with plants from fertilizer plots on the sandy site and with plants outside of test plots at both sites. Allocation was examined using only intact plants; individuals with grazing or root damage were discarded. This selection procedure tended to bias the sample in favor of smaller plants, but appeared to have no effect on estimates of biomass allocation (Bell et al. 1979). Because leaves and stems were both green and presumably photosyn-
thetic, they were treated as a single unit. Reproductive biomass included penducles above the highest leaf. In studies of effects of fertilizers, allocation was determined for combined materials from all individuals of one species in each plot. All other determinations of biomass allocation were based upon 20 individuals of each species at each sampling date. Voucher specimens are deposited in the Herbarium at the University of Nevada, Las Vegas.

Results

Growth Responses to Fertilizers

Responses of winter annuals to application of \( \text{NH}_4\text{NO}_3 \) differed greatly between the two sites (Table 1). On the alluvium, total annual community production showed no significant change following nitrogen treatments. Only two species were abundant enough to allow analysis of individual species' response. Of these, Plantago insularis was unaffected by \( \text{NH}_4\text{NO}_3 \) and Nemacladus glanduliferus showed significant decline in production with increasing nitrogen concentrations. Species diversity also decreased significantly (\( F=3.625; \ p<0.05 \)) from 5.6 species m -2 to 1.5 species m -2. In sandy soil, however, application of \( \text{NH}_4\text{NO}_3 \) stimulated a nearly eight-fold increase in community production (Table 1). This was the result of much larger individual plants rather than of altered density (Table 1). All species except Eri-
gonum trichopes showed significant increases in size. Maximal growth was generally in the plots treated with 10 g N m -2.

Species diversity at the sandy site was not changed by fertilizers.

Experiments in 1977-1978 showed results similar to those of 1978-1979. Total plant production in sandy soil increased by the same proportion in both years, but individual species had somewhat different degrees of response (Table 2). Total production in control and N-treated plots was higher in 1978 than in 1979. Plants in sandy soil were unaffected by application of 5 g P m -2 either alone or in combination with nitrogen.

Tissue Nitrogen Levels

Tissue nitrogen levels were determined during the fruiting state for eleven species. Except in Astragalus sabulonum and Eschscholzia glyptosperma tissue nitrogen concentrations were generally rather low (Table 3), and never exceeded 1.3% in any organ of Cryptantha pterocarya, C. angustifolia, Chaenacitis fremontii, and Schismus arabicus – all species growing in sandy soil and highly responsive to fertilizer treatments. Species on the alluvium had somewhat higher tissue nitrogen contents. In all cases, tissue N concentration was lowest in the roots, highest in fruits; but, in a comparison of all species, no clear relationship existed between absolute nitrogen concentration and the differences of concentration among various organs.

Changes of tissue N levels during development were determined for eight species. The general pattern was a decline in root and shoot nitrogen accompanied by rising concentrations in reproductive structures (Fig. 1). The decline of nitrogen concentrations in vegetative tissues was more pronounced in nitrogen-rich species, except Eschscholzia glyptosperma which retained consistently high shoot N. Two species, Schismus arabicus and Chaenacitis carphoclinia, had falling concentrations of reproductive tissue nitrogen during expansion of flowers and fruits.

Nitrogen concentrations varied little between samples of similar tissues. Differences were 0.01 to 0.05% of dry weight except for Phacelia crenulata whose leaf N concentration appeared to vary with leaf age even on a single plant.

Biomass and Nitrogen Allocation under Natural Conditions

Plant materials collected for an earlier study on seasonal changes in biomass allocation (Bell et al. 1979) were further analyzed for tissue nitrogen concentrations at three stages of their life cycles: bud, flowering (anthesis) and fruiting immediately prior to seed dispersal. Developmental shifts in nitrogen allocation, calculated from biomass allocation and tissue N concentrations, differed considerably among species (Fig. 2). Baileya pentradia and Astragalus sabulonum gradually shifted N into reproductive structures; whereas Chaenacitis carphoclinia showed an abrupt change in allocation with flower development and Plantago insularis a similar shift during fruit maturation. Schismus arabicus showed relatively little change in allocation during the growing season.

A comparison of biomass and N allocation late in fruit development showed that plants invest nitrogen more heavily than