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Chronic nitrogen addition induces a cascade of plant community responses with both seasonal and progressive dynamics

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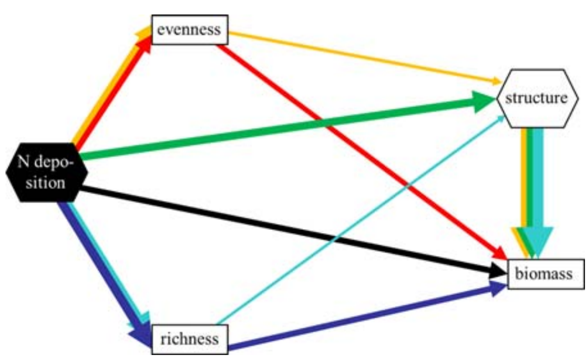
HIGHLIGHTS

- Richness, evenness, density, structure, and productivity change across multiple plant generations in response to N.
- The effect of N deposition on productivity is largely indirect, mediated by changes in richness, evenness or structure.
- Plant community response to N deposition is a cascade of interlinked responses.
- The N deposition response cascade changes through time, obeying both seasonal dynamics and progressive ones linked to duration of exposure to N.

GRAPHICAL ABSTRACT



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ABSTRACT

Short-lived herbaceous plants provide a useful model to rapidly reveal how multiple generations of plants in natural plant communities of sensitive desert ecosystems will be affected by N deposition. We monitored dynamic responses of community structure, richness, evenness, density and biomass of herbaceous plants to experimental N addition (2:1 NH_4^+:NO_3^- added at 0, 0.5, 1, 3, 6 and 24 g N m^{-2} a^{-1}) in three seasons in each of three years in the Gurbantunggut desert, a typical temperate desert of central Asia. We found clear rate-dependent and season-dependent effects of N deposition on each of these variables, in most cases becoming more obvious through time. N addition reduced plant richness, leading to a loss of about half of the species after three generations in the highest N application level. Evenness and density were relatively insensitive to all but the greatest levels of N addition for two generations, but negative effects emerged in the third generation. Biomass, both above and below ground, was non-linearly affected by N deposition. Low and intermediate levels of N deposition often increased biomass, whereas the highest level suppressed biomass. Stimulatory effects of intermediate N addition disappeared in the third generation. All of these responses are strongly interrelated in a cascade of changes. Notably, changes in biomass due to N deposition were mediated by declines in richness and evenness, and other changes in community structure, rather than solely being the direct outcome of release from limitation. The interrelationships between N deposition and the different plant community attributes change not only seasonally, but also progressively change through time. These temporal changes appear to be largely independent of interannual or seasonal climatic conditions.

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1. Introduction

Due to the high intensity of human activities in recent decades – including expansion of agriculture and fertilizer application, and fossil fuel emissions – nitrogen (N) deposition is rapidly increasing globally (Batye et al., 2017; Baez et al., 2007; Galloway et al., 2004). Arid lands cover nearly one third of the terrestrial land surface, and may be highly sensitive to anthropogenic N inputs. After water, N is often considered to be the second most limiting factor to plant growth in global arid lands (Yandjian et al., 2011). Critical N loads of desert ecosystems have been proposed to be lower than other ecosystem types (Brooks, 2003; Fenn et al., 2010), possibly because plant cover is sparse and discontinuous, and, thus natural nutrient pools are small. Thus, arid lands, which by virtue of their low natural soil moisture are already subject to change due to increasing temperatures and potential evapotranspiration, should also be considered vulnerable to the additional anthropogenic forcing of N deposition (Collins and Xia, 2015; Hou et al., 2013; Ladwig et al., 2012; Robertson et al., 2009; Verburg et al., 2013). Specific effects of N deposition are varied and include altered soil microbial activities and N transformation (Liu et al., 2014; Sinsabaugh et al., 2015), altered plant growth and biomass allocation (Zhou et al., 2014), and altered plant community structure and function (Concilio and Loik, 2013; Lan and Bai, 2012; Zeng et al., 2010). Despite an extensive literature on the topic, divergent effects of N deposition on plant communities have been observed and more detailed information of the N effects in arid lands are needed.

Nitrogen affects plant communities in multiple ways. Commonly, the increase in N alleviates the N limitation in sandy and/or arid land soils, increasing the plant productivity and/or density (Li et al., 2015; Plassmann et al., 2009) at rates that vary with the N application rates (Gough et al., 2000; Han et al., 2011). N addition can also induce community structural changes by favoring nitrophiles, and disfavoring competitors or species sensitive to soil chemical changes caused by N addition. For example, N commonly reduces the richness of plant communities and increases the species loss rates (Clark et al., 2013; Gough et al., 2000; Simkin et al., 2016; Su et al., 2013), as nitrophiles become dominant. Increasing degrees of dominance by nitrophiles also lowers evenness of the community (evenness is by definition the opposite of dominance; Mouillot and Lepretre, 1999). Finally, partial community turnover, even without altered richness or evenness, could be induced by favoring some species over others (Plassmann et al., 2009). Community structural changes can go on to influence plant productivity or density via: 1. Complementarity: more efficient use of resources and living space occurs in more species rich communities (Cardinale, 2011; Zeugin et al., 2010), 2. Community trait frequency; communities containing greater proportions of productive or densely-growing species will in turn be more productive or dense than communities containing or dominated by other species (Eskelinen et al., 2012; Schmidt et al., 2015). Thus, the N effect on plant communities is truly a network of interrelated responses.

The spring ephemeral and ephemeroid, and summer annual communities of the Gurbantunggut Desert of China offer an intriguing study system to observe responses to N because: 1. a natural community shift from one flora (spring ephemeral, ephemeroids) to another (summer annuals) occurs over the growing season, and 2. Each season of each year supports a new generation of plants experiencing climates that differ from year to year. Thus, multi-year and multi-season sampling can capture several unique combinations of plant community properties and environmental conditions, over which a N gradient may be superimposed. Ephemerals often germinate and rapidly grow after snow thaw, end their lifecycle before drought seasons, and respond to interannual variation in snow depth. The short vegetative activity of ephemeroids is constrained to the same early season time period, outside of which both roots and shoots senesce and the individual survives as a bulb or tuber. Another group of annuals does not attain peak biomass until August and resists drought seasons. Interannual climate variation can strongly impact these different communities, especially the ephemerals (Fan et al., 2013). In the Gurbantungutt Desert, these temporally variable plant communities play a crucial part in the annual productivity of arid lands. Furthermore, the turnover of these plants can maintain the supply of nutrients in desert soil (Chen and Wang, 2009). Although their biomass may be lower than shrubs in most arid ecosystems, herbaceous ephemeral, ephemeroid, and annual plants cover interspaces between shrubs, greatly reducing spring wind erosion in some areas (Wang et al., 2006). Herbaceous plants also mediate responses of ecosystem C exchange to increased precipitation in a temperate desert (Huang et al., 2015). A change in any of these functions would be significant to the Gubantunggut Desert and downwind ecosystems, but understanding or predicting the response of these highly functional vegetation components to N deposition first requires a multi-year view.

Long-term effects of N addition on plants are of major interest in ecology. Although single season or year effects can explain some trends for perennials, the effects on some ecological processes and plant community structure and function might accrue over the course of many years (Clark and Tilman, 2008; Zhou and Zhang, 2014). In contrast, in ephemeral-annual communities, each year is effectively an observation of an entire generation of individuals, thus a “virtual” long-term study of multiple generations might be achieved in only a few years. We framed a network of hypotheses and tested them by exposing the Gurbantunggut Desert flora to various levels of N deposition, and monitoring plant response both within and among three years. We hypothesized an interrelated cascade of plant responses to N invoking multiple mechanisms (Fig. S1): 1) promotion of nitrophile dominance decreasing richness, decreasing evenness or otherwise inducing species turnover, 2) altered trait dominance, induced by community structural change and leading to altered density (number of individuals per unit area) or productivity, 3) release of N limitation, promoting density and productivity, 4) complementarity in richer communities promoting density or productivity. We proposed multiple, non-mutually exclusive working hypotheses (Chamberlin, 1890) regarding temporal change in these communities: 1. Seasonal: Plant responses to N are primarily determined by season due to a shift from ephemeral-ephemeroid (more sensitive) to long-vegetative annuals (less sensitive), 2. Environmental: Effects of N on the plant community will be determined by environmental variation among sampling times, 3. Progressive: Effects of N on the plant community will increase directionally through time as the cumulative amount of N deposition increases.

2. Materials and methods

2.1. Study area

The Gurbantunggut desert is located in Northwest China. It is the second largest desert in China, with an area of 4.88×10^4 km^2. The mean annual temperature is 8 °C. The annual precipitation is 70–150 mm, about half of which falls between April and July. In winter, an average of 20 cm of snow persistently covers the surface of the desert for 100–160 days. The dominant shrubs in this desert are *Haloxylon persicum* and *H. ammodendron*. In Spring, the snow thaw and increasing temperature provide appropriate conditions for the germination and growth of ephemeral plants (germinating, maturing and flowering in a short time period) and ephemeroid (short-vegetative perennial that persists as a bulb or tuber, with both roots and shoots senescing every year), such as *Erodium oxyrrhynchum* and *Carex physodes*. Some long-vegetative (germinating, maturing and flowering over several months) annual plants, such as *Ceratocarpus arenarius* and *Horanowia ulicina* reach their largest biomass in August. Biological soil crusts are widely distributed on dune slopes and interdunes of the desert, covering about 30% of the total area.