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Responses of tree and insect herbivores to elevated nitrogen inputs: A meta-analysis

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ABSTRACT

Increasing atmospheric nitrogen (N) inputs have the potential to alter terrestrial ecosystem function through impacts on plant-herbivore interactions. The goal of our study is to search for a general pattern in responses of tree characteristics important for herbivores and insect herbivorous performance to elevated N inputs. We conducted a meta-analysis based on 109 papers describing impacts of nitrogen inputs on tree characteristics and 16 papers on insect performance. The differences in plant characteristics and insect performance between broadleaves and conifers were also explored. Tree aboveground biomass, leaf biomass and leaf N concentration significantly increased under elevated N inputs. Elevated N inputs had no significantly overall effect on concentrations of phenolic compounds and lignin but adversely affected tannin, as defensive chemicals for insect herbivores. Additionally, the overall effect of insect herbivore performance (including development time, insect biomass, relative growth rate, and so on) was significantly increased by elevated N inputs. According to the inconsistent responses between broadleaves and conifers, broadleaves would be more likely to increase growth by light interception and photosynthesis rather than producing more defensive chemicals to elevated N inputs by comparison with conifers. Moreover, the overall carbohydrate concentration was significantly reduced by 13.12% in broadleaves while increased slightly in conifers. The overall tannin concentration decreased significantly by 39.21% in broadleaves but a 5.8% decrease in conifers was not significant. The results of the analysis indicated that elevated N inputs would provide more food sources and ameliorate tree palatability for insects, while the resistance of trees against their insect herbivores was weakened, especially for broadleaves. Thus, global forest insect pest problems would be aggravated by elevated N inputs. As N inputs continue to rise in the future, forest ecosystem management should pay more attention to insect pest, especially in the regions dominated by broadleaves.

1. Introduction

As a consequence of accelerated fossil fuel combustion, fertilizer use and anthropogenic nitrogen fixation in recent years, the inputs of reactive nitrogen from the atmosphere to the biosphere continue to increase annually (Deng et al., 2013; Sicard et al., 2016). The impacts of elevated atmospheric nitrogen (N) inputs to terrestrial ecosystems have been recognized, with significant consequences for biodiversity and ecosystem function (Ochoa-Hueso et al., 2013). Elevated N inputs directly affect tree growth and alter physiological processes including N-use efficiency, photosynthesis and biomass accumulation and allocation (Nakaji et al., 2002; Boggs et al., 2007; De Marco et al., 2014). Moreover, concentrations of carbohydrates and nutrients, as well as secondary compounds such as phenolics and terpenoids in various tree species have been reported to increase, decrease or remain the same in response to enhanced N availability (Throop, 2005; Bedison and McNeil, 2009; Wu et al., 2015).

Herbivorous insects that are associated with plant species

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should respond to changes in morphological structures, defensive chemistry and other chemical composition of their host plants (Bobbink et al., 1998). Thus, N input-mediated changes in quality of plant tissues potentially modify plant-herbivore interactions, such as altering insect herbivore performance or outbreak frequency (Pato and Obeso, 2013). Direct effects of elevated N availability on insect performance have been documented, but patterns of such effects are contradictory. For example, Alstad et al. (1982) found enhanced N had detrimental effects on insect growth, while experimental N enrichment in a North American grassland increased total insect abundance (Haddad et al., 2000). The meta-analysis of fertilizers and insect herbivores concluded that application of N fertilizer had a significant positive effect on insect populations (Butler et al., 2012). Waring and Cobb (1992) conducted the first comprehensive review of herbivore performance in N, phosphorus (P), and potassium (K) fertilization studies and found proportionately more negative responses by herbivores to conifers than broadleaf trees and herbs, which meant that conifers would more resistant and/or less attractive to herbivores than flowering plants when fertilized. Therefore, the effects of N inputs on insect herbivore performance are complex and developing generalizations about such processes requires detailed analysis of environmental conditions and species traits.

Forests cover approximately 30% of the global land surface, contain 86% of the earth's aboveground carbon and contribute about 50% of terrestrial net primary production (Bonan, 2008). Increasing N input has the potential to alter forest ecosystem function through its effects on tree-herbivore interactions, with implications for whole terrestrial ecosystems (Curtis and Wang, 1998). Forest ecosystems differ dramatically in composition but are generally of two forms, ‘broadleaved’ (tree composition dominated by angiosperms, either deciduous or evergreen) or ‘coniferous’ (dominated by gymnosperms), which may influence the magnitude and direction of N input effects on plant-herbivore interactions (Gundersen et al., 2009). In particular, it may be useful to explore N input effects on tree palatability and subsequent herbivore effects for different tree types for improved vegetation management in different regions.

To generalize patterns and summarize the differences with respect to elevated N inputs and plant-herbivore interactions and insect herbivore performance in global forest ecosystems, we evaluated and integrated relevant studies from all continents (Lei et al., 2007). These datasets were subjected to meta-analysis, a statistical technique for synthesizing independent results from numerous publications, while avoiding the subjectivity of traditional reviews (Gurevitch and Hedges, 1993). We applied the meta-analysis to develop general patterns in responses of insect herbivores, and tree characteristics important for plant-herbivore interactions, to elevated N inputs. We further investigated the different effects of N inputs on plant characteristics and insect performance in broadleaved vs. coniferous tree types. The following questions are addressed: (1) To what extent would elevated N inputs alter the tree characteristics that influence plant-herbivore interactions? (2) Do elevated N inputs change growth and reproductive performance of insect herbivores? (3) Do the response of tree characteristics and insect performance to N input differ by tree type, specifically broadleaved and coniferous trees?

2. Materials and methods

2.1. Database and suitability criteria

We searched publications listed in lots of science database (including Biosis Previews, China National Knowledge Infrastructure, Elsevier Science, JSTOR, Science online, SpringerLink Journals, Science Citation Index Expanded, Web of Science, Wiley Online Library) during the past three decades (1977–2013) using “nitrogen input”, “nitrogen deposition”, “nitrogen fertilizer” or “nitrogen addition” as keywords, and cross-checked the citations from a large number of nitrogen-related reviews to ensure that the database was comprehensive. We divided all selected data into two groups: the dataset 1 included N input influences on tree characteristics relevant to plant-herbivore interactions (Appendix S1), while the dataset 2 included impacts of N inputs on performance of insect herbivores (Appendix S2).

The meta-analysis was limited to studies that fit the following criteria in the dataset 1: (1) plant species reported in the studies should be trees, excluding studies of shrubs and herbs; (2) data were from experimental manipulations, with appropriate control treatments, using ambient nitrogen condition as compared to experimental treatments with N addition. The added N concentrations, whether in indoor or field studies, were suitable for conversion to corresponding N input levels; (3) the response variables must match at least one of the 23 variables listed in Table 1, which were further classified into two groups consisting of growth and physiological traits or chemical composition variables; (4) the means, measures of variance (e.g. SD, SE or confidence intervals), and the sample sizes of variables in control and experimental groups must be reported in numerical or graphical terms, or be available from the authors (Koricheva et al., 1998); (5) individual observations should be statistically independent, with the following exceptions. Meta-analyses generally assume that individual observations are independent (Ainsworth et al., 2002), and some researchers suggested limiting analysis to only one measurement per treatment of a given species in each study (Curtis and Wang, 1998). However, substantial information was lost by omitting such multiple results (Xia and Wan, 2008), particularly for this meta-analysis which depends upon inclusion of data for the same response variable from more than one elevated N input levels, different plant tissues (e.g. leaf, branch, stem), and/or different growing stages. In this meta-analysis, the measured data of the same variables in all tree aboveground parts (e.g. leaf, branch and stem) and elevated N input levels were utilized. To minimize bias related to lack of full independence of data, when particular response variables of tree species were measured several times within a study, the last sampling date was chosen since global change is a long-term condition (Treseder, 2004). In addition, for the studies that employed trees of different ages, we selected the results from the oldest trees (Zvereva and Kozlov, 2006; Li et al., 2010). Our final database consisted of records from 109 studies reported in 40 different journals. The studies covered a wide taxonomic range, including 70 broadleaved and 26 coniferous species. The selected studies were conducted including a variety of different ways to N input treatment. Except 10.06% no mention of N addition form, it was mainly for the single application of NH_4NO_3 (56.98%), Urea (3.91%), $NaNO_3$ (3.35%) and others (10.06%), while the combined use of two kinds of nitrogen reagents (such as Urea + NH_4NO_3, NH_4Cl + $NaNO_3$, $Ca(NO_3)_2$ + KNO_3, and so on) accounted for 8.94%. Among the collected studies, approximately 59.22% were conducted under field conditions while the rest were performed in growth chambers or greenhouses. Additionally, the studies sites were across a wide range of latitudes, 24 between 0 and 35° latitude (including 35°), 39 between 35 and 45° latitude (including 45°), and 46 at latitudes higher than 45°.

The selection criteria of studies for the dataset 2 was also established as follows: (1) the food resources of insects in the studies must be trees; (2) the experimental manipulations should involve ambient nitrogen levels as the control condition and N addition as the experimental treatment; (3) insect performance variables should include at least one of the following variables: