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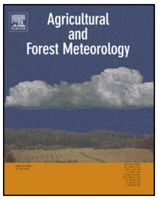

Ephemeral plants mediate responses of ecosystem carbon exchange to increased precipitation in a temperate desert

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ABSTRACT

The ecological consequences of increased precipitation on ecosystem carbon (C) exchange are gaining increasing concern, especially in the context of ongoing climate change in temperate deserts. In this study, a field manipulative experiment was conducted to assess the effects of increased precipitation and nitrogen (N) addition on net ecosystem C exchange (NEE) in a temperate desert in northwestern China during two years with contrasting precipitation patterns (2011 and 2012). Increased precipitation decreased ecosystem C release by nearly 50% in the wet year of 2011, whereas ecosystem C release was increased in the dry year of 2012 because of the disproportional stimulation of gross ecosystem productivity (GEP) and ecosystem respiration (ER) by increased precipitation. N addition had no impact on NEE because of the slight responses of both GEP and ER to N addition. During the wet year, most of the precipitation occurred during the growing season of ephemeral plants, which profoundly stimulated plant growth and led to a higher response of GEP than ER to increased precipitation. As a result, positive effects of increased precipitation on NEE occurred in this year. During the dry year, the majority of the precipitation fell post the ephemeral growing season and only a small increase in herb biomass was observed. However, the response of ER to increased precipitation was larger than that of GEP, leading to a more negative NEE in 2012, as compared to 2011. C release was thus stimulated by increased precipitation in 2012. Irrespective of precipitation treatment, N addition weakly decreased C release because of the negligible stimulation of GEP and ER, as well as the slight response of ephemeral biomass. The responses of NEE to increased precipitation showed no difference between interplant spaces and beneath the dominant shrubs because of the similar responses of plant growth, GEP and ER between sites. Overall, this study shows that the responses of NEE to projected increasing precipitation depend on the coupling of precipitation timing and plant growing season.

1. Introduction

The terrestrial ecosystems are experiencing simultaneous changes in temperature, atmospheric CO_2 concentration, precipitation and nitrogen deposition (IPCC, 2007), and concerns on the ecological consequences of climate change differ among terrestrial ecosystems (Grimm et al., 2013). Precipitation and nitrogen (N) are co-limiting factors in temperate deserts in central Asia (Hooper and Johnson, 1999; Yahdjian et al., 2011). However, climate models predict increasing precipitation (Cholaw et al., 2003; IPCC, 2007) and N deposition (Li et al., 2013; Liu et al., 2013) in these regions. Short-term experiments have shown that both increased precipitation and N deposition can alter vegetation growth and plant community structure (Xia and Wan, 2008; Yahdjian et al., 2011). However, the responses of ecosystem carbon (C) exchange and C budget, as well as their feedbacks to climate change in desert ecosystems, remain unclear because of the few experimental and modeling studies.

Net ecosystem C exchange (NEE) represents the balance between gross ecosystem productivity (GEP) and ecosystem respiration (ER) (Chapin et al., 2002). The responses of GEP and ER to increased precipitation and N are largely dependent on soil moisture and nutrient status in arid and semiarid regions (Huxman et al., 2004; Sponseller, 2007). Increased precipitation can promote GEP by increasing photosynthesis (Yan et al., 2011; Hamerlynck et al., 2012), while its effects on NEE rely on whether ER responds proportionally with GEP. At present, synchronized observations of GEP and ER in temperate deserts are still rare. In addition, the role of desert ecosystems has long been underestimated in the scenario of

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climate change. Therefore, considering the large area and potential C fixation pathways (Evans et al., 2014), further studies are needed to assess their ecological significance.

N deposition due to excessive application of N fertilizers and fossil fuel combustion has become an important subject in global climate change (Tilman et al., 2012). Positive impacts of N addition on individual plant growth are well evidenced in greenhouse experiments (LeBauer and Treseder, 2008), while its effects on plant community and carbon cycling at the ecosystem level are debated in arid and semiarid ecosystems (Hooper and Johnson, 1999; Harpole et al., 2007). The inconsistencies primarily originate from the following three points. First, because of the different directions or divergent magnitudes of responses between GEP and ER to N addition, NEE does not always respond in the same direction as GEP (Hooper and Johnson, 1999). Second, the alteration of plant community structure and composition under N addition can cause complex variations of GEP and ER (LeBauer and Treseder, 2008; Xia and Wan, 2008), leading to uncertain NEE responses to N addition (Xia et al., 2009; Niu et al., 2010). Third, because the degree of N saturation differs among ecosystems, equal amount of N addition may generate contrasting effects on NEE (Fang et al., 2012). In addition, soil N availability usually varies with the precipitation pulse in desert ecosystems (Austin et al., 2004), and N addition effects are dependent on soil moisture (Harpole et al., 2007). Thus, more studies are required to understand the effects of N addition, alone and interactively with increased precipitation, on ecosystem C exchange in desert ecosystems.

GEP and mean annual precipitation are well correlated at the regional scale (Sala et al., 1988; Knapp and Smith, 2001; Reichmann et al., 2013), while their relationship is uncertain at the local scale in arid and semiarid ecosystems (Scott et al., 2009). In addition, soil resources show great variations in interplant spaces and beneath perennial plants (Sponseller, 2007; Cable et al., 2008; Su et al., 2013). Results from manipulative experiments show the rainfall pulses can exert different effects on plants, having no effect on deep-rooted plants and obvious influences on shallow-rooted plants (Snyder et al., 2004; Sponseller et al., 2012; Baez et al., 2013). Thus, vegetation structure may differ in interplant spaces and beneath shrubs, which can generate inconsistent GEP responses to environmental cues. Besides, the relationship between ER and soil moisture also varies in arid ecosystems (Wang et al., 2014). The patchy distribution of shrubs elicits spatial heterogeneities in soil C and N (Jackson and Caldwell, 1993; Aguiar and Sala, 1999). Nutrients accumulate under shrubs, while soil fertility decreases in interplant spaces due to wind erosion and litter movement (Ludwig et al., 2000). The accumulation of nutrients benefits microbial growth under shrubs. Thus, given the close correlation of soil respiration with substrates (Herman et al., 1995; Kieft et al., 1998), ER responses to increased precipitation or N addition may differ between interplant spaces and beneath shrubs. Therefore, incorporating the spatial heterogeneity generated by ‘shrub islands’ into C cycling and budget estimation can increase the prediction accuracy of climate change in desert ecosystems.

The effects of precipitation and N on ecosystem C exchange largely depend on how the dominant functional group responds to changing precipitation and N decomposition and its relative contribution to the ecosystem C exchange (Weltzin et al., 2003; Henry et al., 2006; Suttle et al., 2007). Desert plants have developed different life history strategies to adapt to the highly variable and unpredictable precipitation. For instance, a long life history and slow growth rate are widely observed in perennials and summer annuals, whereas a short life history and fast growth rate occurs in ephemerals and spring annuals, and the two types of plants differ temporally in dominance and biomass in the community. However, the carbon cycling models that consider the relationship of temporal variation in precipitation with plant phenology are still rare (D’Odorico et al., 2003; Moyano et al., 2013; Porporato et al., 2003). In fact, some studies have demonstrated that the ecological consequences of climate change strongly rely on the effects of environmental cues on dominant plant growth (Chou et al., 2008; Heisler-White et al., 2009; Parton et al., 2012; Jongen et al., 2013). Thus, the spatial variation in soil resources between sites and the temporal variation in precipitation may generate complex effects on C exchange in deserts.

Ephemerals (spring annuals) and annual plants (summer and autumn annuals) are two major components of vegetation in the Gurbantunggute Desert, center of the Eurasian Continent (Angert et al., 2010; Fan et al., 2012). Desert ephemerals reach their growth peak within two months after snowmelting, and this peak is a critical phase for herbaceous community in terms of cover and biomass. Annuals exhibit a slow growth rate during ephemeral growing and arrive at the peak growth in late August (Fan et al., 2013). Therefore, herbaceous growth shows apparent ephemeral growing and post ephemeral growing phases (Fig. S1). A field experiment was conducted to investigate the effects of increased precipitation and N addition on NEE and its two components, GEP and ER, in this region in 2011 and 2012. Given the shallow plant roots in this study site, we hypothesized that (1) increased precipitation would increase GEP, imposing positive influences on NEE (smaller CO_2 loss); (2) N addition would increase NEE because of the fertilization effect on plant growth; (3) given that soil moisture can promote plant N uptake, combined increased precipitation and N addition would generate synergistic effects on NEE; (4) both microsite (‘shrub islands’ effect) and the inter- and intra-annual variation of precipitation would regulate the responses of NEE to increased precipitation and N addition.

2. Materials and methods

2.1. Study site description

The field site was in the vicinity of the Fukang Station of Desert Ecology, Chinese Academy of Sciences, on the southern edge of the Gurbantunggut Desert (44°17′ N, 87°56′ E and 475 m a.s.l.). This region has an arid temperate continental climate, with a hot, dry summer and cold winter. The annual mean temperature is 6.6 °C and the annual mean precipitation is 160 mm, of which 70–80% is distributed in the plant growth season from April to September. Soils are desert solonetz, with aeolian sandy soil at the top (0–100 cm). The shrubs and semishrubs are primarily *Tamarix ramosissima*, *Haloxylon ammodendron*, and *H. persicum*, with a coverage of ca. 30%. The herbaceous layer is composed of ephemerals and annuals, with a coverage reaching 40% (Fan et al., 2012). Based on life history, herbs are comprised of two groups: ephemerals (spring-annuals) and annuals (summer-annuals). The dominant ephemerals include *Alyssum linifolium*, *Schismus arabicus*, *Lactuca undulata*, and *Erodium oxyrrhynchum*, accounting for more than 85% of the herbaceous layer biomass. Annuals includes *Salsola subcrassa*, *Ceratocarpus arenarius*, *Orostachys spinosus*, *Euphorbia turczaninowii*, *Descurainia sophia*, *Hyalea pulchella*, *Astragalus arpilobus*, *Trigonella arcuata* and *Agriophyllum squarrosum*, and they are accompanying species from late-March to June, but dominate in the community after the death of ephemerals. Moreover, herbaceous growth season can be divided into two periods in terms of community phenology (Fig. S1). The first period, termed as ‘ephemeral growing season’, is usually before mid-June, and the plant community is dominated by ephemerals. The second period, termed as ‘post ephemeral growing season’, is after ephemeral death, and the plant community is dominated by annuals. According to the phenological protocol (Price and Waser, 1998), the duration of the ephemeral growing season was set from the date