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Verification of a threshold concept of ecologically effective precipitation pulse: From plant individuals to ecosystem

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ABSTRACT

In water-limited ecosystems, an ecologically significant rainfall pulse was defined as a rainfall event that altered both soil water status and plant physiological activity. We developed a new threshold concept of an ecologically effective precipitation pulse (EEPP) applicable to both plant individual and ecosystem scales. The concept was tested in a typical steppe on Inner Mongolia plateau. Two EEPPs, single 3-mm rainfall and 5-mm rainfall, were applied to investigate their effects on soil and plant water status, CO_2 assimilation of five species (four C_3 plants and one C_4 plant), whole-plot soil respiration (R_s), and net ecosystem CO_2 exchange (NEE) on 1 June and 28 July 2009, respectively. Both EEPPs increased leaf water potential (Ψ_l) of all the species, which peaked 1–3 days after rainfall pulses. Soil water content (*SWC*) in two depths (5 cm and 20 cm) significantly increased after the two EEPPs for 1–3 days. Soil water potential (Ψ_s) within 20-cm soil layer in EEPP treatments significantly differed ($p<0.05$) from control. Net assimilation rates (A_{net}) of all C_3 plants had a slight increase at the next day after two EEPPs, in contrast to the C_4 species. R_s elevated and peaked 1–3 days later after water supply. Ecosystem net CO_2 absorption rate rose to maximum value 3 days after the 5-mm pulse on 28 July, higher than the response to 3-mm pulse on June 1. The grassland turned to net emission of CO_2 after 3-mm pulse on 28 July. The results supported that there was an ecosystem level threshold for EEPP, and the threshold was temporally variable. It also highlighted the necessity of considering the response threshold of EEPP in rainfall manipulative experiment. In addition, effective rainfall amount was more approriate than total rainfall amount in modeling ecosystem carbon balance.

1. Introduction

The availability of water, like other resources limiting biological activity, is spatially and temporally heterogeneous in semiarid ecosystems (Lambers et al., 1998). Although most studies focused on the ecological implications of long-term dynamics and short-term water pulses, especially the effect of rainfall variation on net primary productivity in grasslands in relation to regional rainfall gradients (Fay et al., 2003; Lane et al., 1998), few paid attention to determine the threshold of ecologically effective precipitation pulse (EEPP) in dry environments. Currently, rainfall over 5 mm was generally regarded as ecologically important precipitation in semiarid regions (Huxman et al., 2004; Sala and Lauenroth, 1982). More recently, Huxman et al. (2004) and Hao et al. (2010) argued that EEPP was a compound function of ecosystem structure. It should be a dynamic variable following the development of vegetation canopy. The 'two-layer' model and integrated 'pulse-reserve' model were developed and taken as the standard tools for estimation of biologically important precipitation events, emphasizing the thresholds of plant responses (Ogle and Reynolds, 2004; Schwinning et al., 2004). However, there is little direct experimental evidence to prove the existence of ecologically important precipitation threshold.

In semiarid ecosystems, precipitation is low and highly variable (Bailey, 1979). Small rain events that wet surface layers may be ecologically important because fundamental ecosystem processes, such as carbon and mineral nutrient cycles, are active in this layer (Woodmansee et al., 1981). Therefore, small precipitation events were considered as an important resource of ecological significance for semiarid ecosystems (Sala and Lauenroth, 1982). We advanced threshold concept of ecologically effective precipitation pulse from emphasizing plant level responses to change of ecosystem functions. The new EEPP refers to a rainfall event altering soil and plant water status and resulting in discernible variation of ecosystem-atmospheric CO_2 fluxes.

Surprisingly, the ideas of ecologically effective precipitation pulse have not been paid much attention by ecologists, despite common concern on shift of precipitation pattern under global climate change. For example, in precipitation manipulation experiments, rainfall size was set arbitrarily and not explained in details (Huxman et al., 2004; Knapp et al., 2002; Potts et al., 2006). Importantly, in simulating net primary productivity or other ecological processes (for example, Century carbon model and DNDC model), the total amount of rainfall, rather than ecologically effective precipitation, was a main input parameter (Kang et al., 2011; Parton et al., 1993). This will likely overestimate

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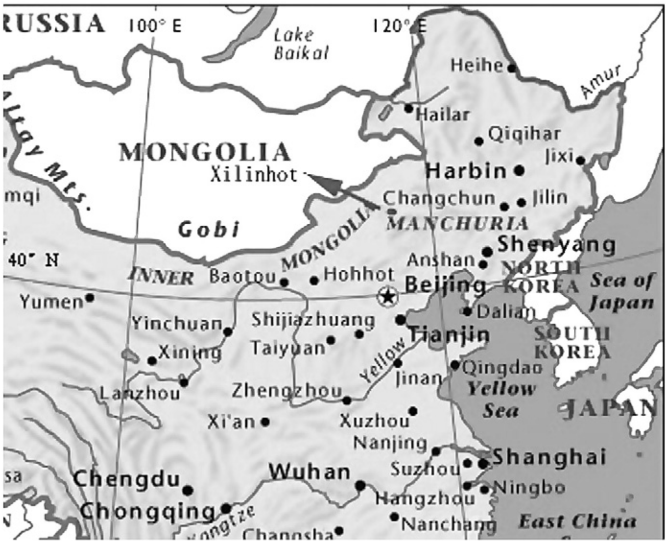

Fig. 1. Distribution of typical steppe in China (after «China Grassland Resource» 1996).

ecosystems productivity. Hence, it is necessary to determine the threshold of ecologically effective precipitation pulse for improvement of carbon cycle model and understanding the effect of water availability on carbon cycle. Our objective was to test the hypothesis that the threshold concept of an ecologically significant rainfall event can be extended to ecosystem level by field experiments.

2. Materials and methods

2.1. Experiment design

The experiment was conducted at the Inner Mongolia Grassland Ecosystem Research Station located in the Xilin River Watershed of the Inner Mongolia Autonomous Region (43°32′N, 116°40′E, 1200 m a.s.l, Fig. 1). The site has been fenced since 1979 and is located in a smooth wide plain with low hills on a 2nd-level basalt platform. The climate is described as temperate semiarid steppe with a dry spring and moist summer. Annual temperature averages −0.4 °C with a growing season length of 150–180 days. The annual precipitation range is 320–400 mm, and 89% of annual precipitation is concentrated in April–September (Jiang, 1985).

The soil type at the experimental site is a dark chestnut (Mollisol) and the soil depth is usually over 1.0 to 1.5 m (Wang and Cai, 1988). The A horizon extends to 0.2–0.3-m depth. There is no obvious $CaCO_3$ layer in the soil profile, and the soil consists of 21% clay, 60% sand and 19% silt. Of the 86 species of flowering plants that belong to 28 families and 67 genera in the site, there are 11 grass species (Jiang, 1985). The xeric rhizomatous grass *Leymus chinensis* is the edificato, and *Stipa grandis* Smirnov, *Koeleria pyramidara* (Lam.) P. Beauv (syn. *K. cristata* (L.) Link) and *Agropyron cristatum* (L.) Gaertn. are the dominant species. The heights of grass clusters are 0.5–0.6 m; coverage averages 30–40% but can reach as high as 60–70% during rainy years. The seasonal peak value of aboveground biomass in 2009 was 152.6 ± 22.3 g m^{-2} in August. LAI increased rapidly during the growing season, from 0.57–0.83 in June, to 0.78–0.92 in July, and the maximum of 1.05 m^2 m^{-2} in early-August.

On 1 June 2009,a 3-mm rainfall event was simulated by applying water to four 2 m × 2 m plots with a hand-held sprayer. The other four plots were used as control and the total eight plots were randomly deployed in the experimental area. There was a 1.5-m buffer zone

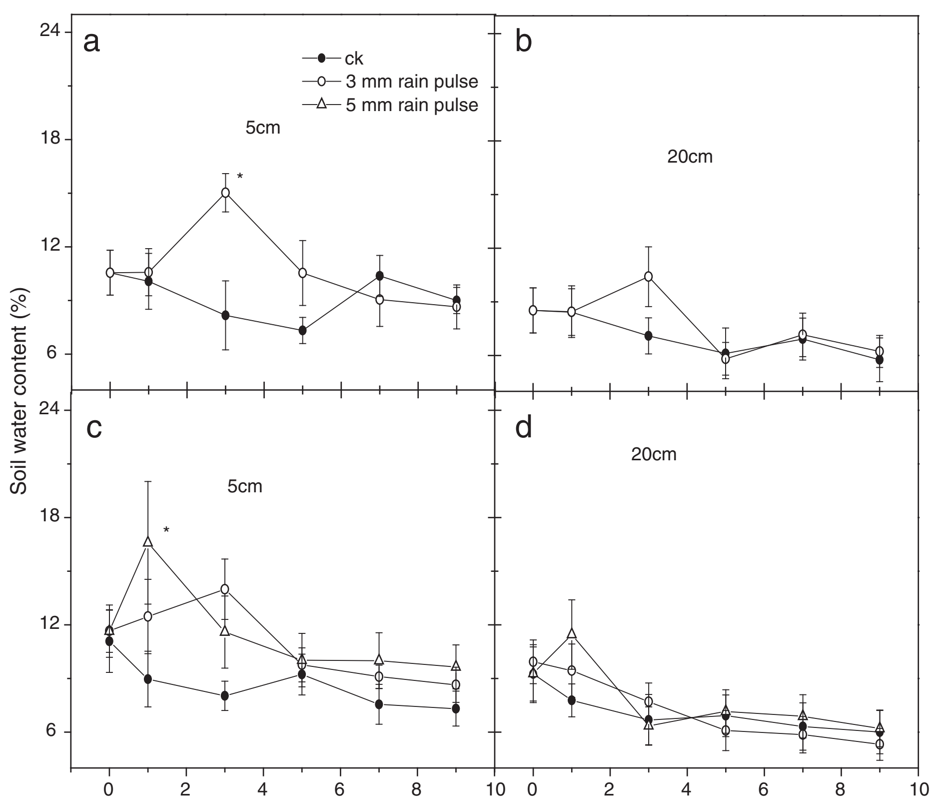

Fig. 2. The dynamics of soil volumetric content in response to a 3-mm precipitation pulse on June 1 (a, b) and a 5-mm precipitation pulse on July 28 (c, d). Data presented were means ± 1SE, for 5- and 20-cm soil depths, respectively. CK is control treatment. * means significant difference in comparison with CK at $\alpha = 0.05$ level.