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Experimental warming drives a seasonal shift of ecosystem carbon exchange in Tibetan alpine meadow

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ABSTRACT

The effects of warming-shifted plant phenology on ecosystem carbon (C) cycling have received increasing attention in recent years. However, there is a lack of evidence and mechanistic understanding of how warming-shifted plant phenology influences ecosystem C cycling. In this study, we conducted a field experiment to investigate the effects of warming on phenology and ecosystem C exchange in a Tibetan alpine meadow during the 2014 and 2015 growing seasons. Our results indicated that warming led to later green-up in spring by aggravating water limitation but little change in autumn phenology, resulting in shortened growing season length. Interestingly, we found warming caused a seasonal shift of ecosystem C exchange. During the early summer monsoon, ecosystem C uptake was suppressed by warming due to the delay of phenological development. However, warming accelerated ecosystem C uptake and promoted ecosystem C uptake under ample water conditions during the late summer monsoon. As a result, although warming shortened the growing season length, it had no significant effects on gross primary production (GPP) and net ecosystem production (NEP). Our results will improve our understanding of the mechanisms of how warming-shifted plant phenology influences ecosystem C cycling in semiarid alpine ecosystems.

1. Introduction

The global mean air temperature has increased continuously since the industrial revolution (IPCC, 2014), and the rising temperatures can impact ecosystem CO_2 exchanges, potentially causing both positive and negative feedbacks to future climates (Luo, 2007; Brient and Bony, 2013). Alpine and arctic ecosystems are believed to be more sensitive to warming because they are experiencing higher than average rates of temperature increases under global climate change (Root et al., 2003; IPCC, 2007). For example, historical climate records show that the Tibetan Plateau has experienced substantial warming in recent decades (i.e., 0.32 °C per decade, Liu and Chen, 2000), and this trend is projected to continue for the future.

The coupled climate-C models predict a positive feedback between terrestrial C cycle and climate warming, primarily due to the increased C release under warming (Friedlingstein et al., 2006). Recent meta-analyses of ecosystem carbon cycle response to warming have also shown that warming increased ecosystem C release (Lu et al., 2013; Wang et al., 2014). However, experiments have shown inconsistent results, with increase (Niu et al., 2013), decrease (Fu et al., 2013; Pendall et al., 2013) or little change (Xia et al., 2009; Chen et al., 2016) in ecosystem respiration–responses that are tied to soil water availability (Pendall et al., 2013), species composition (Niu et al., 2013), and differential responses of the components of ecosystem respiration (Chen et al., 2016).

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Warming can also affect ecosystem C uptake not only directly by changing plant photosynthesis (Luo, 2007), but also indirectly via changing the length of growing season (Sherry et al., 2007; Piao et al., 2007), soil nitrogen mineralization (Melillo and Morrisseau, 2002), soil water availability (Wan et al., 2002), and species composition (Niu et al., 2013). The roles of plant phenology in ecosystem functions, especially on productivity or carbon fluxes, have received increasing attention in recent years (Han et al., 2015). For example, the length of a CO_2 uptake period, or growing season length (GSL), is suggested to have significant direct effects on vegetation dynamics, carbon gains and losses (Wan et al., 2005; Piao et al., 2007; Richardson et al., 2009; Xia and Wan, 2013; Xia et al., 2015).

Globally, warming often leads to earlier flowering in spring and later senescence in autumn (Parmesan and Yohe, 2003; Root et al., 2003), indicating an extended period of active plant growth under warmer conditions. The extension of growing season may serve as one of the important mechanisms in enhancing ecosystem production under climate warming (Nemani et al., 2003). For example, some studies have revealed a positive dependence of net primary production (NPP) upon growing season length over the past decades (Churkina et al., 2005; Piao et al., 2007). However, the positive impact of prolonged growing season on NPP has been challenged in recent years because other processes under climate warming can counteract or reverse the positive impacts of warming-shifted plant phenology on ecosystem C uptake (Xia and Wan, 2013). For example, although earlier flowering improves plant fitness, summer drought associated with climate warming can reduce reproductive success of plant species (Giménez-Benavides et al., 2007) and potentially cancel out the C uptake of terrestrial ecosystem (Angert et al., 2005). In addition, the enhanced respiration by autumn warming can weaken the CO_2 uptake enhancement induced by earlier growing season under spring warming (Piao et al., 2008). Moreover, advanced budbreak under warming may lead to injury from late-spring frost and longer leaf retention and increase the risk of freezing damage in the autumn (Norby et al., 2003). All these studies suggest that the mechanism of warming effects on plant growth and terrestrial NPP is complex and that the influences of lengthening growing season on ecosystem C sequestration may be regulated by other biotic and abiotic factors associated with climate warming (Xia and Wan, 2013).

Plant phenology is strongly influenced by warming in alpine and Arctic ecosystems. Warming can have divergent consequences on plant phenology, including advanced (Dunne et al., 2003; Cleland et al., 2006), delayed (Hollister et al., 2005; Yu et al., 2010) or unchanged (Hoffmann et al., 2010) phenological events. By shifting phenological stages, warming can significantly extend or shorten the length of growing season which may lead to differential responses of how ecosystem carbon exchange to climate warming. To enhance our understanding of warming-shifted plant phenology influences ecosystem C cycling, we conducted a field experiment to investigate the effects of warming on phenology and ecosystem C exchange in a semiarid alpine meadow on the Tibetan Plateau since 2014. Three major questions were addressed: (i) How does warming influence the phenology and growing season length? (ii) What are the impacts warming-shifted plant phenology on ecosystem C exchange? (iii) What are the mechanisms underlying the above two processes?

2. Material and methods

2.1. Study area

The study area was located in a typical alpine meadow grassland at Naqu, northern Tibet, China (31°38.513′ N, 92°0.921′ E), approximately 4600 m in elevation. The mean annual temperature is −1.2 °C. The mean annual precipitation is 430 mm, with precipitation occurring mainly during the summer season from June to September. The Asian monsoon is the main source of precipitation in this region (Dorji et al., 2013). The onset of the summer monsoon over the past nearly 60 years has a mean date of 22 May (DOY: 142 ± 14), however, there is considerable annual variation. Winter precipitation, which typically falls as snow, is low in this region (Dorji et al., 2013). The growing season normally starts in mid-May and lasts until mid-September. The vegetation is dominated by *Kobresia pygmaea*, accompanied by *Potentilla saundersiana*, *Potentilla cuneata*, *Stipa purpurea*, *and Festuca coelestis*.

2.2. Study design

Beginning in 2014, open-top chambers (2.0 m high and 1.5 m along the bottom edge) were used to evaluate the effects of warming on the alpine meadow ecosystem, with three replicate chambers for both the control and warming plots. In the warming plots, chambers were placed before growth started in early April, and removed at the end of the growing season in October. In the control plots, open chambers without transparent plastic sheet were placed and removed in the same way. Soil temperature and moisture at 5 cm belowground were monitored with the Decagon EC-TM sensors (Decagon Devices, Pullman, Washington, USA). Measurements were taken every 1 h for all sensors.

2.3. Ecosystem C fluxes measurements

Ecosystem C fluxes were measured in a subplot in each plot from May to September in 2014 and 2015. In each subplot, one square aluminum frame ($0.5 \times 0.5\,m^2$) was permanently inserted into the soil at 4 cm depth. Each side of the frame was 2 cm wide and provided a flat base between the soil surface and the CO_2 sampling chamber (the chamber refitted by Niu et al., 2010). Ecosystem C exchange was measured with an infrared gas analyzer (IRGA; LI-6400, LiCor Inc., Lincoln, Nebraska, USA) attached to a transparent chamber ($0.5 \times 0.5 \times 0.5\,m^3$), which covered all the vegetation within the aluminum frame. The radiation is reduced by 10% within the chamber, which was measured by a Licor sensor (Licor-2003S). One small electric fan was running continuously to promote air mixing within the chamber during the measurement.

Thirty consecutive recordings of CO_2 concentration were taken from each frame at 3-s intervals during a 90-s period after steady-state conditions were achieved within the chamber. During measurement, CO_2 concentration was allowed to build up or draw down over time, from which flux rates were determined from the time-course of the concentration to calculate net ecosystem production (NEP). Increases in air temperatures within the chamber during the measuring time period were about 0.5 °C. Details about these static-chamber flux calculations can be found in the soil-flux calculation procedure on the LI-6400 manual (LiCor Inc., 2004). Following measurement of NEP, the chamber was vented, replaced on each frame, and covered with an opaque cloth. Then the CO_2 exchange measurements were repeated. Because the second set of measurements eliminated light (and hence photosynthesis), the values obtained represented ecosystem respiration (ER). The difference between NEP and ER was considered to represent instantaneous GPP for the vegetation within the chamber. Measurements of ecosystem gas exchange were made twice each month at 9 am–12 pm in 2014. In 2015, ecosystem gas exchange was measured at 5-day intervals at 9:00–12:00 am