Agriculture, Ecosystems and Environment 220 (2016) 152–163

Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

journal homepage: www.elsevier.com/locate/agee

Carbon and water flux patterns of a drought-prone mid-succession ecosystem developed on abandoned karst grassland

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ARTICLE INFO

Article history:
Received 16 August 2015
Received in revised form 9 January 2016
Accepted 14 January 2016
Available online 21 January 2016

Keywords:
Ecological succession
Afforestation
Eddy covariance
Post-drought recovery
Light response curves
Rain-use efficiency
Calcareous substrate

ABSTRACT

Successional ecosystems developed spontaneously on agricultural lands cover a substantial area worldwide, particularly in Europe and North America. The functioning of these ecosystems in terms of carbon and water fluxes remains fairly under-investigated. Here, carbon and water exchanges of a spatially heterogeneous tree-shrub-grassland mosaic developed on former semi-dry calcareous grassland in the sub-Mediterranean region of Slovenia were studied. Using eddy covariance, the annual, seasonal and daily dynamics of net ecosystem exchange (NEE) and water vapor exchange were examined, together with their environmental controls during the period August 2008–December 2012. Over this period, the ecosystem appeared to be a carbon sink but the annual carbon fixation had a span of more than four-fold, from 82 to 351 $g\,C\,m^{-2}\,yr^{-1}$. This variability was largely explained by different durations of drought events that occurred during the summer despite the high and relatively evenly distributed rainfall. This is related to the poor ecosystem rain use efficiency, only 0.10–0.35 $g\,C\,m^{-2}\,yr^{-1}$ was taken up per mm of rain and the estimated deep water drainage ranged between 44 and 72% of the incoming rain. Drought periods were identified by deriving the critical soil water content (SWC) (here 0.145 $m^3\,m^{-3}$) at which evapotranspiration and carbon fluxes started to be limited by water availability. The estimated annual gross primary productivity was shown to be linearly dependent on the duration of the longest annual drought period and not on the drought intensity. Despite a severe drought in the summer of 2012, the ecosystem proved quite resilient to drought stress and restored its carbon uptake after several rain events. As shown by the light response curves, the light dependency of carbon exchange was affected by seasonality and environmental factors, particularly SWC, vapor pressure deficit (VPD) and air temperature (Ta). Interaction between the factors was also observed; negative effect of low SWC was significantly enhanced in the conditions of higher Ta or higher VPD.

1. Introduction

In terms of matter and energy exchanges, ecosystems are often seen as relatively discrete units—forests, croplands, grasslands or wetlands, which predominantly respond to ambient environmental factors (Piao et al., 2009; Reichstein et al., 2007). Many ecosystems, however, possess a stronger legacy of past events (e.g., Bond-Lamberty et al., 2013; Coursolle et al., 2012) and can be regarded as successional, i.e., changing their predominant vegetation character through time. The ecology of these ecosystems is still understudied, despite the fact that they cover an important area globally. Among these, succession ecosystems thriving on former agricultural land but developing mostly spontaneously without active planting or seeding of trees, cover a substantial area (Knapp et al., 2008; Ramankutty and Foley, 1999). In Europe, according to FAOSTAT (2014), 12.9% of agricultural areas have been abandoned in the last forty years, with southern (Mediterranean) Europe being the most affected. Land abandonment is also widespread in eastern North America and former Soviet countries (Cramer et al., 2007). During the last decades, these marginal areas for agriculture have been overgrown by trees and shrubs (MacDonald et al., 2000; Hall et al., 2002; Kaligarič et al., 2006). In view of global change, these lands might gain additional value in national greenhouse gas (GHG) balance accounts as potential sites for carbon sequestration and/or sites of bioenergy production (Potter et al., 2007). On the other hand, the expansion of woodland/shrubland areas could jeopardize the underground and watershed water quantities (increased water

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http://dx.doi.org/10.1016/j.agee.2016.01.020
0167-8809/

depletion due to higher transpiration losses), reduce regional or landscape biodiversity (homogenisation of the landscape, loss of transitional ecosystems with their specific communities) (Ratajczak et al., 2012) and increase wildfire hazards.

Expansion of woody vegetation is presumed to increase the net carbon sink of such successional ecosystems (Post and Kwon, 2000) and their demand for water (Scott et al., 2006). During a succession, carbon accumulates as living woody biomass (Knapp et al., 2008), as soil organic matter (Laganiere et al., 2010) or both (Grünzweig et al., 2007; Thuille and Schulze, 2006). Reported sequestration potentials are in the range of 40–120 g C m^{-2} yr^{-1} in boreal regions, of 150–450 g C m^{-2} yr^{-1} in temperate regions, and of 400–800 g C m^{-2} yr^{-1} in tropical regions (IPCC, 2003 and references therein). However, the sequestration potential of spontaneously overgrown ecosystems somewhat differs from the potential of human-induced afforestations. Afforestations, in which the vegetation composition is regulated naturally, have substantially less carbon sink capacity than afforested plantations (Stoy et al., 2008). In a comparison of different agricultural land, larger soil sinks were reported for abandoned arable land than for pastures and grasslands (Laganiere et al., 2010). Jackson et al. (2002) even showed a decrease in soil organic carbon reserves in woodland ecosystems developed spontaneously from former low productive grassland, particularly if developed in more humid climatic conditions. However, grasslands more often lose carbon only within the first few years of woody plant encroachment (Vesterdal et al., 2011; Coursolle et al., 2012).

Various factors determine the overall carbon budget of abandoned and overgrown agricultural land, such as climatic and soil conditions, vegetation properties, spatial patterns of woody encroachment, etc., but detailed understanding of the impact of these factors to carbon balance is still lacking. As shown in a cross-continental analysis (Knapp et al., 2008), annual precipitation largely governed the shifts of carbon stocks (aboveground) during the grassland–shrubland transition; in xeric conditions the carbon gain was negative but it substantially increased in more humid areas. Soil characteristics largely determine the successional path and ecosystem performance, too. Many abandoned areas are located in environments with shallow, stony soils or on steeper terrain where water availability and drought often determine the ecosystem productivity, even in regions with relatively abundant rainfall, such as in karst areas (Ferlan et al., 2011; Liu et al., 2013). In years with prolonged or intensified drought, the carbon sink of successional savannah-like ecosystems is often diminished; they may even become C sources (Kolb et al., 2013; Pereira et al., 2007; Ma et al., 2007). However, their overall tolerance to drought and their post-drought regeneration of sink activity are often larger than under the previous agricultural system (Ferlan et al., 2011; Potts et al., 2006b), mainly due to the higher effectiveness of woody plant species in water absorption (rooting depth) and transport.

In this study, the carbon and water fluxes over a patchy successional ecosystem—developed on former calcareous grassland after the cessation of grazing ca. 50 years ago—were examined using ecosystem level measurements (with the eddy covariance (EC) technique). Since this ecosystem is prone to drought, its fluxes are particularly evaluated with respect to water availability. More specifically, the objectives of our study were: (1) to evaluate the annual and seasonal variability of C fluxesover a period of more than four years, (2) to explain the effects of the main environmental drivers on the observed patterns of ecosystem C exchange, (3) to determine summer drought onset, severity and interactions between drought and other environmental factors (light, temperature, vapor pressure deficit) and (4) to investigate rain-pulse effects and post-drought regeneration of C uptake.

2. Materials and methods

2.1. Study area

The study was conducted on the Podgorski kras plateau (45° 32′ N; 13° 55′ E; 400–430 m a.s.l.) in the sub-Mediterranean region of Slovenia (SW of the country). The climate is transitional between Mediterranean and the continental climates, which means more humid conditions, colder winter and less pronounced drought periods during summer than under a Mediterranean climate. The mean annual temperature of the 30-year period (1980–2010) was 10.5 °C and the average annual rainfall 1280 mm. The predominant soil type is rendzic cambisol (rendzina) lying on limestone bedrock. Rocks occupy more than 50% of the soil volume of the upper 40 cm of the soil profile. Sheep, goat and cattle grazing was practised here until the mid-20th century, when agricultural activities ceased and the grasslands were slowly overgrown by trees and shrubs. The vegetation is uneven, with patches of woody plants interspersed by grassy gaps. In the woody plant layer, pubescent oak (*Quercus pubescens* Willd.), manna ash (*Fraxinus ornus* L.), common juniper (*Juniperus communis* L.) and smoketree (*Cotinus coggygria* Scop.) prevail; the species-rich grass layer is dominated by upright brome (*Bromopsis erecta* (Huds.) Fourr.), dwarf sedge (*Carex humilis* Leyss.) and tor grass (*Brachypodium rupestre* (Host) R.&S.). The average height of the tree layer is 7 m; the mean cover of woody species is roughly 55%. The vegetation of the site is mid-successional, meaning that it is composed of species of the former successional stage (calcareous grassland (*Carici humilis-Centaureetum rupestris*)) and of species of the potential natural vegetation of the area (*Ostryo carpinifoliae-Quercetum pubescentis*). With the ongoing succession toward the potential vegetation, the tree canopy is expected to be denser (>80% tree cover) with tree heights up to 12–15 m. A more detailed description of the study area can be found in Ferlan et al. (2011).

2.2. Eddy covariance and meteorological measurements

An eddy covariance tower was installed within the central part of the study area in July 2008. Despite the overall flat terrain, some sinkholes 10–30 m in diameter and 2–8 m in depth were present within the tower footprint area but they were densely covered or surrounded by woody species and presumably had no major impact on wind direction and wind speed. An open-path eddy covariance system consisting of an open path infrared gas (CO_2 and H_2O) analyser (IRGA) (LI-7500, Li-Cor, Lincoln, NE, USA) and a sonic anemometer (CSAT3, Campbell Scientific, Logan, UT USA) were installed at 15 m. The LI-7500 was pointed toward the north at an angle of 20° to minimise solar radiation influence and to facilitate the shedding of water droplets from sensor lenses after rain events. Data from the sonic anemometer and the open path infrared gas analyser were recorded at a frequency of 20 Hz using a CR3000 data logger (Campbell Scientific, Logan, UT, USA).

Additionally, some meteorological sensors were installed at or next to the flux tower. Soil temperature (in °C) was measured at −10 cm using two sets of thermocouples (TCAV, Campbell Scientific, Logan, UT, USA) and soil water content (SWC, in m^3 m^{-3}) at −10 cm with two time domain reflectometers (CS616, Campbell Scientific, Logan, UT, USA) inserted horizontally. Incident global radiation (Rg, in W m^{-2}) (LP02, Campbell Scientific, Logan, UT, USA), incident photosynthetic flux density (PPFD, in μmol m^{-2} s^{-1}) (LI-190, Li-Cor, Lincoln, NE, USA), net radiation (in W m^{-2}) (NR-LITE, Campbell Scientific, Logan, UT, USA), air temperature (Ta, in °C), and relative humidity (in %) (HMP45AC, Vaisala, Helsinki, Finland), soil heat flux (in W m^{-2}) at −10 cm using two soil heat flux plates (HFP01SC, Campbell Scientific, Logan, UT, USA) and precipitation (in mm) (Rain gauge, Davis, Hayward, CA, USA) were