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Effects of frequency and intensity of drying-rewetting cycles on *Hydrocotyle vulgaris* growth and greenhouse gas emissions from wetland microcosms

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A R T I C L E I N F O

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A B S T R A C T

Drying-rewetting cycles can affect ecosystem functioning, but little is known about how the interact[redacted] frequency and intensity of drying-rewetting cycles affects greenhouse gas emissions from plant-soil [redacted] assembled microcosms initially each having two vegetative individuals (ramets) of a clonal, w[redacted] *Hydrocotyle vulgaris*, and subjected them to three frequencies (6, 9 and 18 cycles with 9, 6 and 3 da[redacted] crossed with three intensities (adding 200, 400 and 600 ml water per cycle) of drying-rewettin[redacted] 54 days. Increasing frequency of drying-rewetting cycles significantly increased growth and net ph[redacted] rate of *H. vulgaris* under the lowest intensity of drying-rewetting cycles, but decreased them or h[redacted] under the two higher intensities. Increasing drying-rewetting frequency significantly increased C[redacted] under the lowest intensity and decreased it under the highest intensity, whereas no effect was foun[redacted] intermediate intensity. CO_2 emission was positively related to growth of *H. vulgaris*. Under the low[redacted] CH_4 emission was not significantly affected by frequency, but under the two higher intensities it wa[redacted] in the highest frequency. Under the lowest intensity N_2O emission was the highest in the highest fr[redacted] it was not affected by frequency under the two higher intensities. Therefore, frequency and intensi[redacted] rewetting cycles can interact to affect greenhouse gas emissions from plant-soil systems. Prolonged [redacted] frequency of precipitation) can decrease CO_2 emission under a lower amount of precipitation, bu[redacted] under a higher amount of precipitation.

1. Introduction

Global climate change is predicted to alter patterns of precipitation and increase frequencies of extreme climate events such as drought and flood (IPCC, 2013; Reichstein et al., 2013). As a result, surface soils will undergo more frequent drying-rewetting cycles (Seneviratne et al., 2010). Changes in these unprecedented drying-rewetting cycles may greatly impact plant growth, population dynamics, community structure and ecosystem function (Estop-Aragones and Blodau, 2012; Niu et al., 2014; Zeppel et al., 2014; Wilcox et al., 2015; Estop-Aragones et al., 2016).

Frequency and intensity of drying-rewetting cycles are two important determinants of the effects of drying-rewetting cycles on ecosystem functioning (Knapp et al., 2002; Ciais et al., 2005; Breda et al., 2006; Schwalm et al., 2010; Shi et al., 2014). Reducing frequency of larger rainfall events, for instance, reduced aboveground net primary productivity of grassland ecosystems, but increased soil CO_2 flux (Knapp et al., 2002). Altering frequency of drying-rewetting cycles also changed the magnitude of greenhouse gas emissions by affe[redacted] biomass and rhizodeposit quantity of crops (Zhu and Che[redacted] Moreover, soil drying frequency induced by plant transpi[redacted] could impact plant growth and rhizodeposit quantity, whic[redacted] ther affect rhizosphere priming and responses of soil orga[redacted] decomposition to drying-rewetting cycles (Zhu and Cheng[redacted] wetlands, changing frequency of drying-rewetting cycles m[redacted] crease plant-soil respiration and greenhouse gas emissio[redacted] proving soil aerate function (Wang et al., 2009; Gao et[redacted] Maucieri et al., 2017a). However, few studies have teste[redacted] frequency of drying-rewetting cycles on greenhouse gas emi[redacted] plant-soil systems in wetlands (Niu et al., 2014; Liang et al[redacted]

Changes in intensity of drying-rewetting cycles can also alter ecosystem functioning (Ciais et al., 2005; Breda et al., 2006; Schwalm et al., 2010; Shi et al., 2014; Sun et al., 2016). In grassland ecosystems, vegetative productivity generally increased with rainfall intensity (Huxman et al., 2004; Shi et al., 2014; Zhang et al., 2017). In temperate deciduous Beech and northern Mediterranean forest ecosystems, severe

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drought events during drying-rewetting cycles decreased their primary productivity, canopy conductance and ecosystem respiration (Ciais et al., 2005). Drying-rewetting cycles affect stomatal conductance, leaf area and plant respiration by altering soil moistures in temperate forest ecosystems (Breda et al., 2006). Schwalm et al. (2010) found that global ecosystem respiration was sensitive to a drought event by analyzing observational data from a global network of eddy flux towers, and gross ecosystem productivity was 50% more sensitive to a drought event than ecosystem respiration (Schwalm et al., 2010).

Frequency and intensity of drying-rewetting cycles may interact to affect ecosystem functioning (Niu et al., 2014; Estop-Aragones et al., 2016). Under low to intermediate level of intensity of drying-rewetting cycles, high frequency may be more important because high frequency may maintain soil water content and facilitate plant growth. By contrast, under a high level of intensity, high frequency may be of little importance because redundant soil water is maintained, which may inhibit plant growth, change microbial composition and activity and thus inhibit CO_2 emission and promote CH_4 emission due to soil saturation (Gao et al., 2016; Zhang et al., 2017). So far, however, little is known about the interactive effect of frequency and intensity of drying-rewetting cycles on greenhouse gas emissions from plant-soil systems.

To test how patterns of drying-rewetting cycles affects greenhouse gas emissions from plant-soil systems, we artificially assembled microcosms with a model plant *Hydrocotyle vulgaris* L. (Araliaceae; Dong et al., 2013, 2015). *H. vulgaris* is clonal perennial herb originating from Europe where it is commonly distributed in moist habitats (Murphy et al., 1990). This species was introduced to China as an ornamental aquatic plant, but has been widely naturalized (Miao et al., 2011). *H. vulgaris* can reproduce quickly by producing creeping stems along which each node can root and form a leaf and an axillary bud that will develop into a new creeping stem (Dong et al., 2013, 2015). Due to such vigorous clonal growth, populations of *H. vulgaris* expand quickly so that in some wetlands in China *H. vulgaris* has become a problem weed, blocking rivers and canals and replacing native species (Miao et al., 2011).

We subjected the *H. vulgaris* microcosms to three frequencies (6, 9 and 18 cycles with 9, 6 and 3 days per cycle) and three intensities (adding 200, 400 and 600 ml water per cycle) of drying-rewetting cycles for 54 days. We aimed to test the following two hypotheses: (1) increasing intensity of water supply increases growth of *H. vulgaris*, but this effect is altered by frequency of drying-rewetting cycles; (2) intensity and frequency of drying-rewetting cycles interact to affect greenhouse gas emissions from the microcosms.

2. Materials and methods

2.1. Experimental microcosm set-up

Plants of *H. vulgaris* were collected from Xixi wetland in Hangzhou, Zhejiang Province, China, and propagated vegetatively in a greenhouse at Forest Science Co. Ltd. of Beijing Forestry University in Beijing. We selected 100 similar-sized vegetative individuals (ramets) of *H. vulgaris*, and each ramet had a node, a leaf and a few roots. Ten of them were randomly selected [illegible]

Table 1
Effects of frequency and intensity of drying-rewetting cycles on growth of *H. vulgaris* and greenhouse gas emissions of the microcosms.

Variable	Frequency (F)		Intensity (I)		F × I	
	$F_{2,36}$	P	$F_{2,36}$	P	$F_{4,36}$	P
Biomass	0.76	0.474	**30.10**	**< 0.001**	**23.74**	**< 0.001**
No. of ramets	0.72	0.493	**19.14**	**< 0.001**	**23.18**	**< 0.001**
Leaf area	**5.24**	**0.010**	2.91	0.067	**15.59**	**< 0.001**
Photosynthesis rate	**6.14**	**0.005**	**6.84**	**0.003**	**4.37**	**0.006**
CO_2 emission	0.16	0.850	**10.67**	**< 0.001**	**12.89**	**< 0.001**
CH_4 emission	**5.26**	**0.011**	**4.33**	**0.022**	0.56	0.696
N_2O emission	0.43	0.656	0.64	0.533	**3.41**	**0.021**

The given are *F*, degree of freedom and *P* of two-way ANOVAs. Values with *P*

transformation was needed. We used two-way ANOVA to examine effects of water supply frequency and intensity of drying-rewetting cycles and their interaction on biomass, number of ramets, leaf area and net photosynthesis rate of *H. vulgaris* and emissions of CO_2, CH_4, and N_2O from the plant-soil systems in the microcosms. Regression was used to examine the relationships of emissions of CO_2, CH_4, and N_2O with biomass, number of ramets and leaf area of *H. vulgaris*. We used Tukey tests for multiple comparisons. The analyses were conducted with SPSS 18.0 (SPSS Inc., Chicago, IL, USA).

3. Results

3.1. Effects of frequency and intensity on plant growth

There was a highly significantly interactive effect of frequency and intensity of drying-rewetting cycles on growth and net photosynthesis rate of *H. vulgaris* (Table 1). Under the low intensity treatment, biomass, number of ramets and leaf area were significantly higher in the high than in the low and the medium frequency treatment (Fig. 1A–C), and net photosynthesis rate was larger in the high than in the low frequency treatment (Fig. 1D). Under the medium intensity treatment, however, high frequency significantly decreased biomass, number of ramets and leaf area, but did not affect net photosynthesis rate of *H. vulgaris* (Fig. 1). Under the high intensity treatment, high frequency significantly decreased biomass and leaf area, but did not affect number of ramets or net photosynthesis rate (Fig. 1).

3.2. Effects of frequency and intensity on greenhouse gas emissions

There was a highly significant effect of frequency and intensity on CO_2 emission from the *H. vulgaris* microcosms (Table 1). Under the low intensity treatment, CO_2 emission was significantly higher in the high frequency treatment than in the medium and low frequency treatments (Fig. 2A). Increasing frequency of drying-rewetting cycles significantly decreased CO_2 emission under the high intensity treatment, but had no significant effect under the medium intensity treatment (Fig. 2A). CH_4 emission was significantly higher in the high than in the low and the medium frequency treatment under the high intensity treatment, and was also significantly higher in the high than in the medium frequency treatment under the medium intensity treatment (Table 1, Fig. 2B). However, CH_4 emission did not differ significantly between the three frequency treatments under the low intensity treatment (Fig. 2B). N_2O emission was significantly higher in the high than in the medium and low frequency treatment under the low intensity treatment, but did not differ significantly between the three frequency treatments under the medium and the high intensity treatment (Table 1, Fig. 2C).

3.3. Relationships between greenhouse gas emissions and plant growth

CO_2 emission was significantly positively related to biomass ($R^2 = 0.56$, $P < 0.001$), number of ramets ($R^2 = 0.49$, $P < 0.001$) and leaf area ($R^2 = 0.40$, $P < 0.001$) of *H. vulgaris*, but not to net photosynthesis rate ($R^2 = 0.06$, $P = 0.135$, Fig. 3). In contrast, neither CH_4 emission ($R^2 = 0.001$–0.008, $P = 0.58$–0.84) nor N_2O emission ($R^2 = 0.04$–0.08, $P = 0.09$–0.22) was significantly related to biomass, number of ramets or leaf area of *H. vulgaris*.

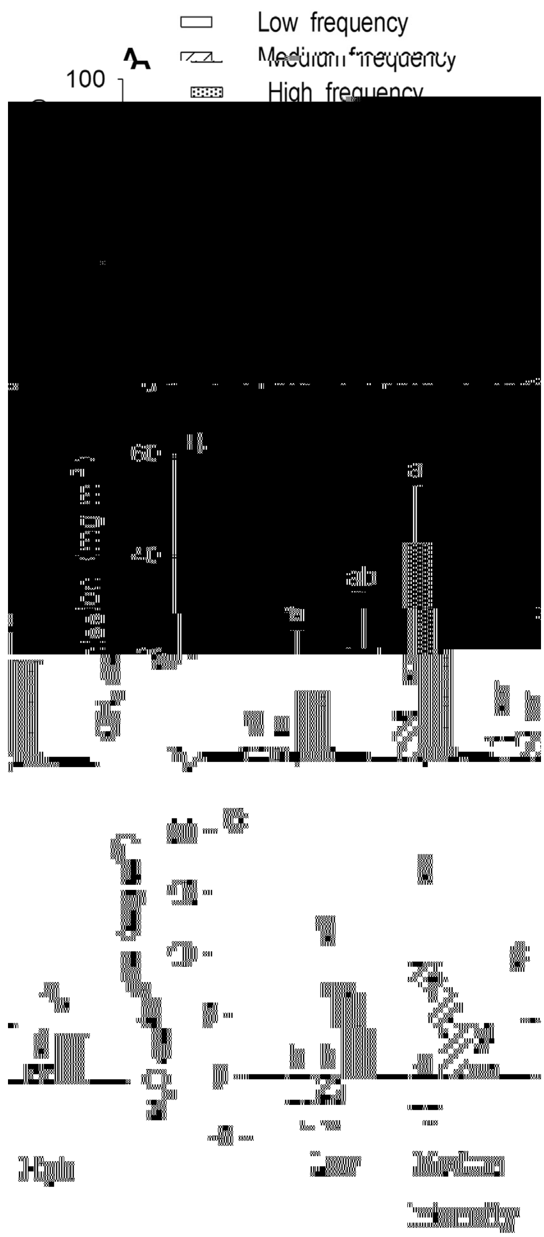

Fig. 2. Effects of frequency and intensity of drying-rewetting cycles on cumulative emissions of CO_2 (A), CH_4 (B) and N_2O (C) from the microcosms during the 54 days of the experiment. Bars and vertical lines represent means and SE ($n = 5$). With each level of intensity, different letters indicate that means differ significantly among the frequency treatments (by Tukey tests).

4. Discussion

We found that increasing frequency of drying-rewetting cycles promoted growth and clonal reproduction of *H. vulgaris* under low intensity of drying-rewetting cycles, but decreased them or had no significant effect under medium and high intensity. Previous studies showed that increasing frequency increased net photosynthesis and aboveground net primary productivity of grassland ecosystems (Knapp et al., 2002; Fay et al., 2003; Heisler-White et al., 2009). This was in accordance with our results under low intensity of water supply, and implied that high frequency of water supply promoted the water utilization efficiency of the *H. vulgaris* communities. Wilcox et al. (Wilcox et al., 2015) showed that decreasing frequency had different effects on above- and belowground net primary productivity in semiarid and mesic grassland ecosystems. Specifically, more xeric grasslands were more sensitive to frequency of precipitation than more mesic grasslands (Huxman et al., 2004; Heisler-White et al., 2009; Knapp et al., 2015). The mechanism is that other resources become more limiting to ecosystem processes so that sensitivity to alterations in precipitation decreases when intensity of precipitation increases (Huxman et al., 2004). We found that the highest frequency inhibited growth of *H. vulgaris* with medium and high water supply intensity. This was likely because *H. vulgaris* had to adapt to the inundation environment repeatedly.

Increasing frequency promoted CO_2 emission from the *H. vulgaris* microcosms with low water supply intensity (corresponding to 0.6 ± 0.07 to $1.4 \pm 0.12\ g\ m^{-2}\ d^{-1}$), but decreased or had no effect with medium and high water supply intensity. Such an interactive effect of frequency and intensity of dry-rewetting cycles on CO_2 emission was consistent with the effect on growth of *H. vulgaris*. Consequently, CO_2 emission was significantly positively related to growth of *H. vulgaris*. These results suggest that CO_2 emission from the *H. vulgaris* microcosms may mainly derive from shoot and root respiration of *H. vulgaris*, and/or from fast respiration from easily degraded organic matter in the root exudate, agreeing with the findings of previous studies (Zhang et al., 2009; Hirota et al., 2010; Laine et al., 2012; Mo et al., 2015). The positive relationship between CO_2 emission and biomass also indicates that CO_2 emission from plant-soil systems may be predicted indirectly by biomass of plant communities (Zhang et al., 2009; Hirota et al., 2010; Mo et al., 2015) which is much easier to measure compared to CO_2 emission.

Higher frequency promoted CH_4 emission under higher water supply intensity, but CH_4 emission was not related to biomass of *H. vulgaris*. Previous studies showed that CH_4 emission were influenced by temperature and soil water content which affected the production of substrate precursors and microbial activity (Beringer et al., 2013). Higher frequency maintained higher soil water content which benefited methanogenic bacteria in the soil (Joabsson and Christensen, 2001; Ding et al., 2005). The fairly short delays for the recovery of methanogens with high frequency may be related to an adaption of the communities to oxygen stress (Estop-Aragones and Blodau, 2012).

Increasing frequency promoted N_2O emission from the *H. vulgaris* microcosms under low water supply intensity, but had no effect under medium and high water supply intensity. N_2O production was mainly controlled by soil nitrification and denitrification processes, which were mainly affected by environmental factors such as soil temperature, water content and soil nutrient levels (Beringer et al., 2013). N_2O emission generally occurs with suitable soil moisture of 90%–100% or water-filled pore space of 70%–90% (Zheng et al., 1997; Welzmiller et al., 2008). In our study, the soil moisture was very likely to differ between the frequency and intensity treatments, but it might not reach an appropriate range of 90%–100% during the most period of the experiment. Thus N_2O emission did not show significant difference under medium and high water supply intensity. This was accordance with previous studies showing that increasing soil moisture did not significantly affect N_2O emission due to its complex and multiple routes of formation (Hu et al., 2015; Maucieri et al., 2017b).

We conclude that frequency and intensity of drying-rewetting cycles can interact to affect greenhouse gas emissions from ecosystems. Prolonged drought (low frequency of precipitation) due to future climatic change may decrease CO_2 and N_2O emissions under a lower amount (intensity) of precipitation, but may promote CO_2 and CH_4 emissions under a higher amount of precipitation.

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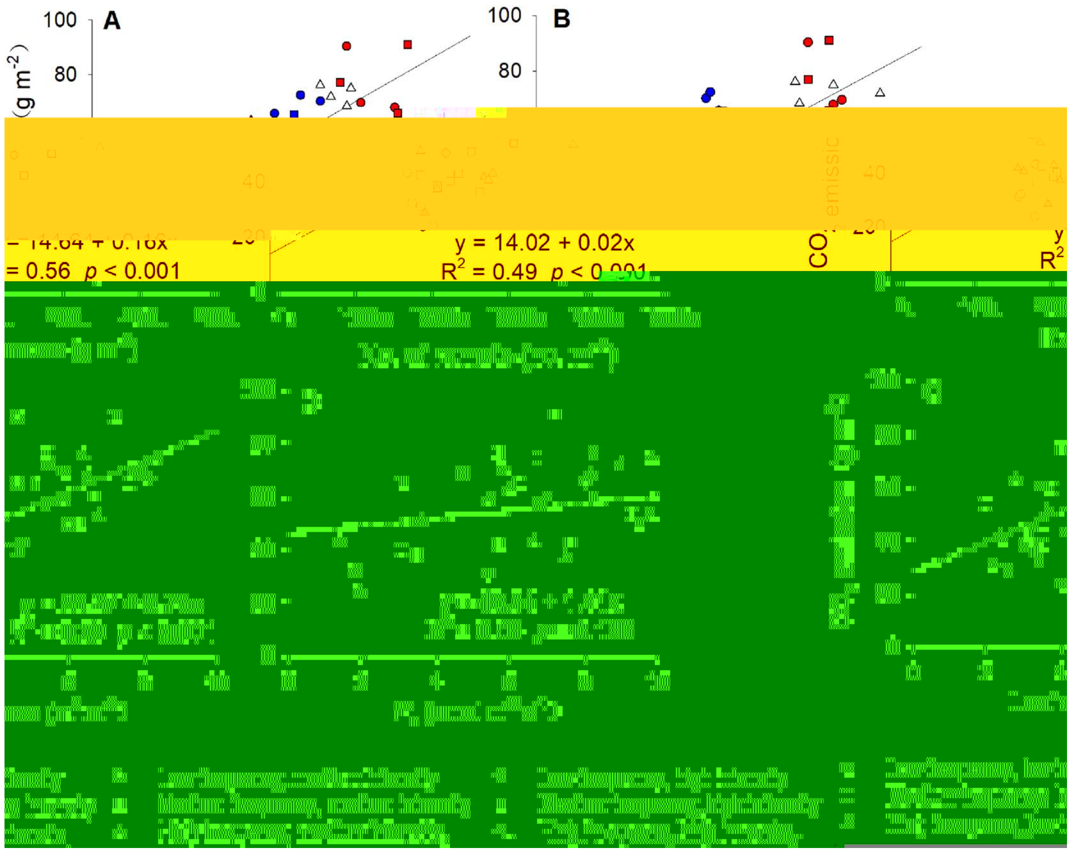

Fig. 3. Relationships between CO_2 cumulative emission and growth of *H. vulgaris* during the 54 days of the experiment. The scattered points represent data measured in each microcosm.

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