



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

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ABSTRACT

Drying-rewetting cycles can affect ecosystem functioning, but little is known about how the interaction between frequency and intensity of drying-rewetting cycles affects greenhouse gas emissions from plant-soil systems. We assembled microcosms initially each having two vegetative individuals (ramets) of a clonal, wetland plant *Hydrocotyle vulgaris*, and subjected them to three frequencies (6, 9 and 18 cycles with 9, 6 and 3 days per cycle) crossed with three intensities (adding 200, 400 and 600 ml water per cycle) of drying-rewetting cycles for 54 days. Increasing frequency of drying-rewetting cycles significantly increased growth and net photosynthesis rate of *H. vulgaris* under the lowest intensity of drying-rewetting cycles, but decreased them or had no effect under the two higher intensities. Increasing drying-rewetting frequency significantly increased CO₂ emission under the lowest intensity and decreased it under the highest intensity, whereas no effect was found under the intermediate intensity. CO₂ emission was positively related to growth of *H. vulgaris*. Under the lowest intensity CH₄ emission was not significantly affected by frequency, but under the two higher intensities it was the highest in the highest frequency. Under the lowest intensity N₂O emission was the highest in the highest frequency, but it was not affected by frequency under the two higher intensities. Therefore, frequency and intensity of drying-rewetting cycles can interact to affect greenhouse gas emissions from plant-soil systems. Prolonged drought (low frequency of precipitation) can decrease CO₂ emission under a lower amount of precipitation, but promote it 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; Ciaies 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 CO₂ flux (Knapp et al., 2002). Altering frequency of drying-rewetting cycles also

changed the magnitude of greenhouse gas emissions by affecting plant biomass and rhizodeposit quantity of crops (Zhu and Cheng, 2013). Moreover, soil drying frequency induced by plant transpiration rate could impact plant growth and rhizodeposit quantity, which may further affect rhizosphere priming and responses of soil organic matter decomposition to drying-rewetting cycles (Zhu and Cheng, 2013). In wetlands, changing frequency of drying-rewetting cycles may also increase plant-soil respiration and greenhouse gas emissions by improving soil aeration function (Wang et al., 2009; Gao et al., 2016; Maucieri et al., 2017a). However, few studies have tested effects of frequency of drying-rewetting cycles on greenhouse gas emissions from plant-soil systems in wetlands (Niu et al., 2014; Liang et al., 2016).

Changes in intensity of drying-rewetting cycles can also alter ecosystem functioning (Ciaies 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 CO₂ emission and promote CH₄ 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 and dried to measure initial dry mass (0.13 ± 0.01 g, mean \pm s.e.). The remaining 90 ramets were grown in 45 pots (16 cm in diameter and 20 cm in depth) filled with an even mixture of sand and commercial compost (Meishimei Bio-Tech Co. Ltd., Beijing, China) at an 1:1 volume ratio. The sand-compost mixture contained 80 mg C g⁻¹, 4.75 mg total N g⁻¹ and 2.83 mg total P g⁻¹. The soil used was within the broad range of the wetland soil in nature, which could also ensure that plants grew well during the experiment. Each pot was planted with two ramets of *H. vulgaris*.

2.2. Experimental design

The experiment was a factorial design with three levels of water

supply intensity (low, medium and high) crossed with three levels of water supply frequency (low, medium and high) of drying-rewetting cycles. For low, medium and high water supply intensity, we added 200, 400 and 600 ml water, respectively, to the pot per drying-rewetting cycle. For low, medium and high water supply frequency, there were 6, 9 and 18 drying-rewetting cycles during the experiment, with 9, 6 and 3 days per cycle, respectively. The amount of 200 ml water every three days corresponded approximately to the rate of supply of the annual mean precipitation (1400 mm) in Hangzhou where *H. vulgaris* was collected (Wu et al., 2012). There were five replicates (pots) for each treatment. There was no water above the soil surface in any frequency in the low intensity treatments, about 2 cm above the soil surface immediately after water was added each time in the high frequency and high intensity treatment, and about 0.5 to 1.5 cm above the soil surface immediately after water was added each time in all other treatments. The water level changed with time and there was no water above the soil surface 2–3 days later after water was added each time.

The experiment started on 10 July and ended on 2 September 2015, lasting 54 days. It was conducted in the same greenhouse where *H. vulgaris* was cultivated. During the experiment, the air temperature was 27–36 °C and the relative humidity 40–60%. The photosynthetically active radiation measured at the plant level at noon was 300–500 mmol photons m⁻² s⁻¹. The containers were randomly repositioned three times during the experiment to avoid potential effect of acclimatization in microenvironments.

2.3. Measurements

We measured emissions of CO₂, CH₄ and N₂O from the microcosms (pots with soil and ramets) between 09:00 to 11:00 AM every 9 days using static closed chambers (15.8 cm in inner diameter and 50 cm in inner height) made of opaque PVC. The chambers were each installed with a small fan for air circulation. For measurements, the chambers first enclosed the microcosms and were sealed for 60 min, and greenhouse gas emissions from the plant-soil systems were then captured.

Headspace samples (40 ml) were taken at 0, 30 and 60 min with syringe and were analyzed within 24 h for CO₂, CH₄ and N₂O concentrations using a modified gas chromatography (GC Agilent 7890A, Agilent Technologies, Santa Clara, CA, USA) equipped with flame ionization detectors and electron capture detectors. Gas emission was calculated according to the equation (Song et al., 2008; Wang et al., 2013):

$$F = \frac{dc}{dt} \cdot \frac{M}{V_0} \cdot \frac{P}{P_0} \cdot \frac{T_0}{T} \cdot H$$

where F is gas emission, $\frac{dc}{dt}$ is the slope of the curve of gas concentration versus time, M is the mole mass of the gas, P and P_0 are the atmospheric pressure in situ and under standard conditions, T and T_0 are the absolute temperature in situ and under standard conditions, H is the relative height of the column above the water surface, and V_0 is the mole volume of the gas under standard conditions. Cumulative emission was calculated as the mean of the emissions on each pair of consecutive sampling days multiplied by the time interval between them (Johnson et al., 2006; Begum et al., 2014).

At harvest, we counted number of ramets of *H. vulgaris*, and measured leaf area (WinFOLIA Pro 2004a, Regent Instruments, Inc., QC, Canada). Net photosynthetic rate (P_n) was measured at a CO₂ concentration of 400 μmol mol⁻¹ and a photo flux density of 1200 μmol m⁻² s⁻¹ using a Li-6400 photosynthesis system (Li-Cor Biosciences, Lincoln, NE, USA). Then, plant material was dried at 70 °C for 72 h and weighed. Plant dry mass was expressed as g m⁻².

2.4. Data analysis

Before analyses, the data on growth and greenhouse gas emissions were checked for normality and homogeneity of variance, and no data

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	
	<i>F</i> _{2,36}	<i>P</i>	<i>F</i> _{2,36}	<i>P</i>	<i>F</i> _{4,36}	<i>P</i>
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 ₂ O 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* < 0.05 are in bold.

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 CO₂, CH₄, and N₂O from the plant-soil systems in the microcosms. Regression was used to examine the relationships of emissions of CO₂, CH₄, and N₂O 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,

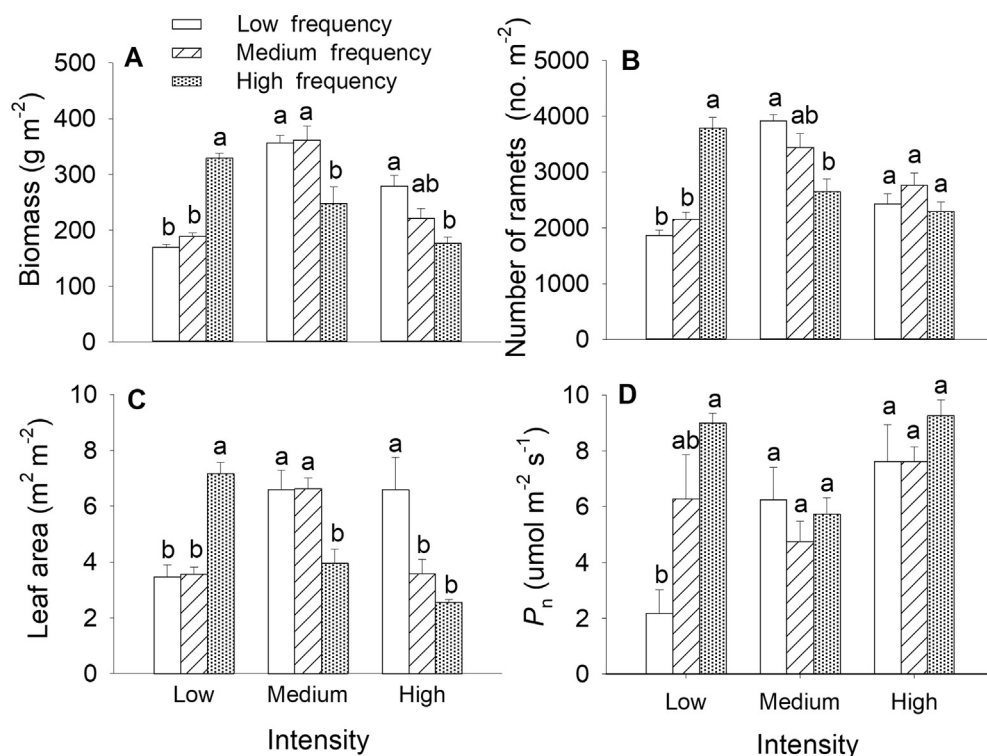


Fig. 1. Effects of frequency and intensity of drying-rewetting cycles on (A) biomass, (B) number of ramets, (C) leaf area and (D) net photosynthesis rate (*P_n*) of *H. vulgaris*. Bars and vertical lines represent means and SE (*n* = 5). With each level of intensity, different letters indicate that means differ significantly among the frequency treatments (by Tukey tests).

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 CO₂ emission from the *H. vulgaris* microcosms (Table 1). Under the low intensity treatment, CO₂ 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 CO₂ emission under the high intensity treatment, but had no significant effect under the medium intensity treatment (Fig. 2A). CH₄ 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, CH₄ emission did not differ significantly between the three frequency treatments under the low intensity treatment (Fig. 2B). N₂O 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

CO₂ 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 CH₄ emission (*R*² = 0.001–0.008, *P* = 0.58–0.84) nor N₂O 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*.

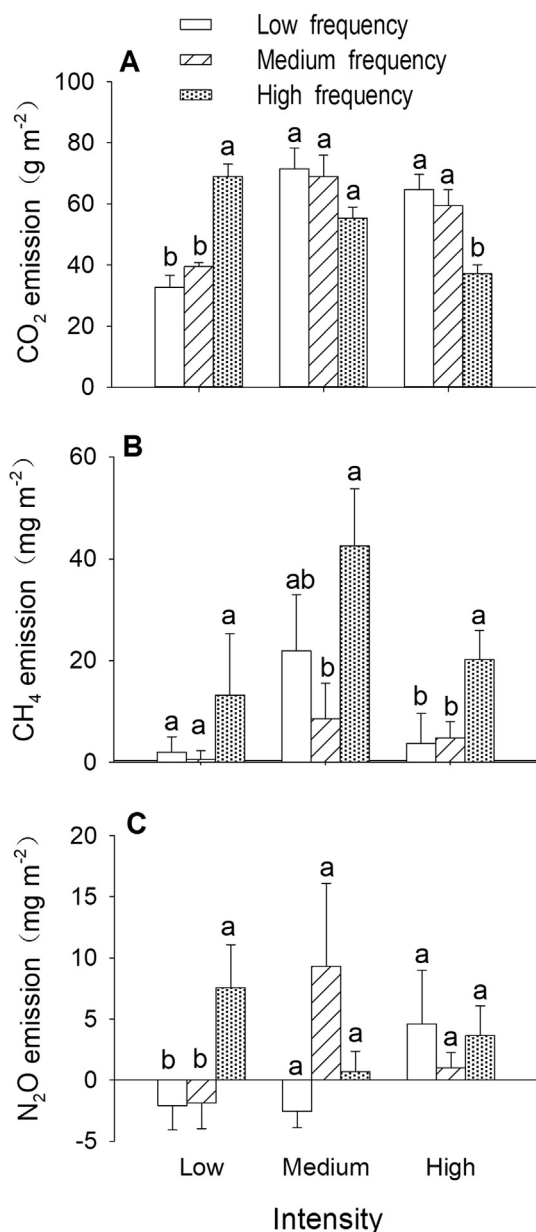


Fig. 2. Effects of frequency and intensity of drying-rewetting cycles on cumulative emissions of CO₂ (A), CH₄ (B) and N₂O (C) from the microcosms during the 54 days of the experiment. Bars and vertical lines represent means and SE ($n = 5$). With each level of intensity, different letters indicate that 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 CO₂ emission from the *H. vulgaris* microcosms with low water supply intensity (corresponding to 0.6 ± 0.07 to $1.4 \pm 0.12 \text{ g m}^{-2} \text{ d}^{-1}$), 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 CO₂ emission was consistent with the effect on growth of *H. vulgaris*. Consequently, CO₂ emission was significantly positively related to growth of *H. vulgaris*. These results suggest that CO₂ 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 CO₂ emission and biomass also indicates that CO₂ 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 CO₂ emission.

Higher frequency promoted CH₄ emission under higher water supply intensity, but CH₄ emission was not related to biomass of *H. vulgaris*. Previous studies showed that CH₄ 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 adaptation of the communities to oxygen stress (Estop-Aragones and Blodau, 2012).

Increasing frequency promoted N₂O emission from the *H. vulgaris* microcosms under low water supply intensity, but had no effect under medium and high water supply intensity. N₂O 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). N₂O emission generally occurs with suitable soil moisture of 90%–100% or water-filled pore space of 70%–90% (Zheng et al., 1997; Welzmler 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 N₂O 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 N₂O 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 CO₂ and N₂O emissions under a lower amount (intensity) of precipitation, but may promote CO₂ and CH₄ emissions under a higher amount of precipitation.

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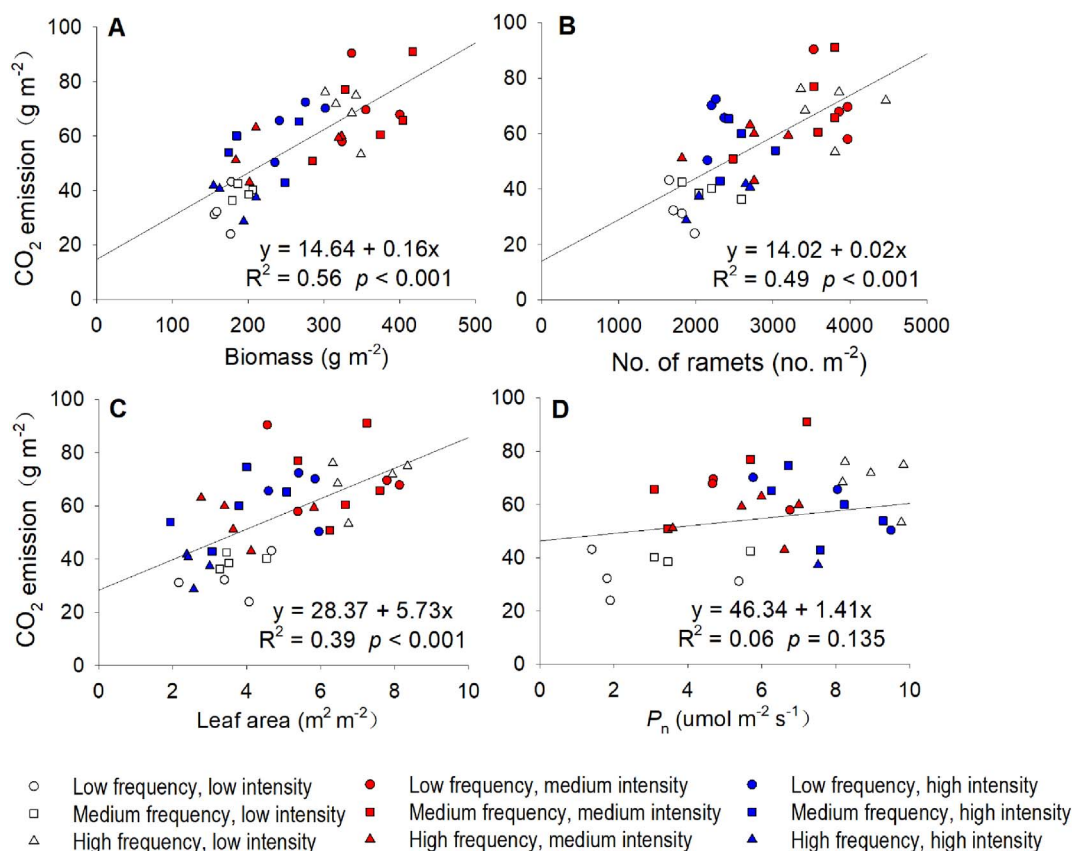


Fig. 3. Relationships between CO₂ cumulative emission and growth of *H. vulgaris* during the 54 days of the experiment. The scattered points represent data measured in each microcosm.

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