Effects of temporal heterogeneity in nutrient supply on intra- and inter-genet competition of a clonal herb

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A B S T R A C T

Nutrients are often released heterogeneously over time (e.g., in pulses) in natural habitats. Different genotypes of the same plant species may vary in their responses to temporal nutrient heterogeneity so that temporal nutrient heterogeneity may influence intraspecific interactions. To test effects of temporal nutrient heterogeneity on intra-genet (competition between ramets of the same genotype) and inter-genet competition (competition between ramets of different genotypes), we conducted a greenhouse experiment with five genotypes of the clonal herb *Hydrocotyle vulgaris*. We grew one ramet (no competition), two ramets of the same genotype or two ramets of different genotypes in a pot and supplied the pot with the same total amount of nutrients either homogeneously or heterogeneously. Results showed that temporal nutrient heterogeneity affected the growth and biomass allocation of some genotypes, but had no impact on those of other genotypes of *H. vulgaris*. These suggested that responses to temporal nutrient heterogeneity were different between genotypes of *H. vulgaris*. Temporal nutrient heterogeneity had little effect on intra-genet competition of *H. vulgaris* likely because ramets of the same genotype did not differ in their responses to temporal nutrient heterogeneity. However, temporal nutrient heterogeneity increased the competitive ability of the genotype of *H. vulgaris* with higher plant productivity. We conclude that temporal nutrient heterogeneity can influence intraspecific interactions of the clonal plant *H. vulgaris* by altering inter-genet competition, and this effect may further change population dynamics of the plant.

1. Introduction

Resources (e.g., nutrients and water) are often released heterogeneously over time (i.e., in pulses) in natural habitats (James and Richards, 2005; Padilla et al., 2013; Wang et al., 2016; Yu et al., 2019; Slate et al., 2021). For example, in arid and semi-arid ecosystems, soil water availability is pulsed because discrete rainfall events are commonly interspersed with drought periods (Austin et al., 2004; Chesson et al., 2004; Schwinning et al., 2004; Chen et al., 2009). In these ecosystems, soil nutrients are also often available to plants in brief pulses following precipitation events (Noy-Meir, 1973; James and Richards, 2005; Schaeffer and Evans, 2006).

Plant species may vary in response to temporal resource heterogeneity (Gebauer et al., 2002; He et al., 2012; Lu et al., 2016). For

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example, water and nutrient pulses were found to increase (Maestre and Reynolds, 2007; Osone et al., 2014; Yuan et al., 2017), decrease (Hagiwara et al., 2010, 2012) or have no effects on (Gebauer et al., 2002; Tsunoda et al., 2014; Wang et al., 2015) plant growth. As a result, temporal heterogeneity in resource supply may promote the competitive ability of plant species that respond positively to it, reduce the competitive ability of those that respond negatively, or have no effects on the competitive ability of those that show no response. Consequently, temporal resource heterogeneity may alter interspecific interactions of plants and further influence species coexistence, community structure and ecosystem functions (Gebauer et al., 2002; He et al., 2012; Lu et al., 2016; Chen et al., 2019).

Similarly, genotypes within species may vary in their responses to temporal resource heterogeneity. This might be expected to affect intraspecific competition much as plant species differently respond to temporal resource heterogeneity affects interspecific competition (Gebauer et al., 2002; Lu et al., 2016). If different genotypes of the same species respond differently to temporal resource heterogeneity, then temporal resource heterogeneity can alter intraspecific interactions and thus have population-level effects. So far, however, we know little about whether different genotypes within species can respond differently to temporal heterogeneity in resource supply and how temporal resource heterogeneity affects intraspecific interactions of plants (Wang et al., 2015).

Clonal plants are widespread in natural habitats and play an important role in the maintenance of ecosystem functions (Song and Dong, 2002; Benson and Hartnett, 2006; Roiloa et al., 2010; Dong, 2011; Klimešová et al., 2021). Effects of temporal heterogeneity in resource supply on intraspecific competition could be particularly important in some clonal plants as they often form clusters or even monodominant stands (Aguilera et al., 2010; Travis et al., 2010). Clonal plant populations commonly consist of multiple genets (differing in genotypes), and each genet can have a number of ramets (sharing the same genotype) (Harper, 1977; Clarke, 2012). Thus, intraspecific interactions of clonal plants are comprised of both intra-genet interactions (i.e., interactions between ramets of the same genotype) and inter-genet interactions (i.e., interactions between ramets of different genotypes; de Kroon et al., 1992; Gruntman and Novoplansky, 2004; Semchenko et al., 2007).

Ramets from the same genotype are expected to behave similarly so that they are most likely to respond similarly to resource heterogeneity (Zhou et al., 2012). Therefore, we hypothesize that temporal resource heterogeneity will not influence intra-genet interactions of clonal plants. With the same species, ramets from different genotypes can respond differently to resource heterogeneity (Alpert, 1999; van Kleunen and Fischer, 2001), but this is not always the case (Lotscher and Hay, 1997). If ramets from different genotypes do not differ significantly in their responses to temporal resource heterogeneity, then temporal resource heterogeneity will also not alter inter-genet interactions of clonal plants. In contrast, if ramets from different genotypes vary greatly in their responses to temporal resource heterogeneity, then temporal resource heterogeneity will alter inter-genet interactions. To our knowledge, no study has tested the effects of temporal heterogeneity in resource supply on intra- vs. inter-genet interactions of clonal plants.

To test the effects of temporal nutrient heterogeneity on intra- and inter-genet competition of clonal plants, we conducted a greenhouse experiment with five genotypes of the clonal herb *Hydrocotyle vulgaris*. We grew one ramet (no competition), two ramets of the same genotype (with intra-genet competition) or two ramets of different genotypes (with inter-genet competition) in a pot with homogenous nutrient supply (giving nutrients continuously, i.e., once every day) or heterogeneous nutrient supply (giving nutrients in pulses, i.e., once per week). The total amount of nutrients added were the same for all the pots. Specifically, we tested the following hypotheses: (1) different genotypes of *H. vulgaris* can vary in their responses to temporal nutrient heterogeneity, (2) temporal nutrient heterogeneity has no impact on intra-genet competition of *H. vulgaris*, and (3) temporal nutrient heterogeneity can alter inter-genet competition of *H. vulgaris*.

2. Materials and methods

2.1. Species information and preparation

Hydrocotyle vulgaris L. is a perennial clonal herb of the Araliaceae family and is widely distributed across many temperate and tropical regions of the world (Liu et al., 2017; Si et al., 2020). It was introduced to China as an ornamental plant in the 1990 s and is considered to be an invasive species (Miao et al., 2011). This species can grow in a broad range of habitats, such as aquatic, wet and terrestrial (Dong et al., 2015; Miao et al., 2018). *Hydrocotyle vulgaris* can propagate vegetatively and form large clone by producing creeping stems. Each node along creeping stems has the potential to develop into a ramet with commonly a simple leaf and some adventitious roots (Dong, 1995; Liu et al., 2016).

As detailed in Wang et al. (2020), *H. vulgaris* were collected from 10 sites in southeastern China in 2016 and taken to a greenhouse at Taizhou University in Taizhou, Zhejiang Province, China for vegetative propagation. Sampling locations ranged from 22 to 31° N and 106 2° W. Genotypes of these plants were identified by amplified fragment length polymorphism (AFLP) using genomic DNA (Wang et al., 2020).

On 24 June 2018, five genotypes (coded as A, B, C, D, and E) were randomly selected and propagated vegetatively in plastic boxes (64 cm long × 42 cm wide × 14 cm deep) filled with an 1:1 (v/v) mixture of peat and sand. On 26 July 2018, 120 stem fragments (each having a node and two internodes of 1.5 cm long each) per genotype were cultivated individually in pots (10 cm in diameter × 8 cm in height) filled with the peat-sand mixture. After three weeks, each node had produced a new stem with 3–4 new nodes. We cut off the second node (from the apex) with its connected two internodes from each of these new stems, so that all these isolated nodes were in the same ontogenetic stage. For each genotype, 70 similar-sized ramets were selected and used for the experiment described below.

2.2. Experimental design

The experiment consisted of a total 40 treatments, i.e., 20 competition treatments (no competition, intra-genet competition and inter-genet competition) crossed with two soil nutrient treatments (temporally homogeneous or heterogeneous nutrient supply) (Fig. 1). For the treatment of no competition, one ramet was grown in a pot, resulting in five treatments for the five genotypes (coded as A, B, C, D and E). For intra-genet competition, two ramets of the same genotype were grown in a pot, resulting in also five treatments (AA, BB, CC, DD and EE). For inter-genet competition, two ramets from two different genotypes were grown in a pot, resulting in ten treatments (AB, AC, AD, AE, BC, BD, BE, CD, CE and DE). In the homogeneous treatment, 50 mL of 0.1 g L^{-1} water-soluble fertilizer (Peters Professional, 20% N, 20% P_2O_5, 20% K_2O, Scotts Company, USA) was supplied to each pot every day. In the heterogeneous treatment, 50 mL of 0.7 g L^{-1} water-soluble fertilizer was supplied to each pot every week. Thus, the total amount of nutrients in the homogeneous and heterogeneous treatments was exactly the same. For the treatments of no competition, one ramet was planted in the central part of each pot filled with 5 L of a 1:1 (v/v) mixture of peat and sand, and for the treatments with intra- or inter-genet competition, two ramets were planted around the central part of the pot and spaced 5 cm apart. Each of the 40 treatments was replicated five times, resulting in a total of 200 pots with 350 ramets.

The pots were randomly placed on a bench in a greenhouse at Taizhou University, and repositioned two times during the experiment. Water was added to each pot regularly to keep the soil moist. The experiment started on 15 August, ended on 23 October 2018, and lasted for 10 weeks. Mean air temperature and humidity in the greenhouse during the experiment were 25.3°C and 87.3%, respectively, as measured by Hygrochron temperature loggers (iButton DS1923; Maxim Integrated Products, USA). Photosynthetic photon flux density was 789–1326 µmol m^{-2} s^{-1} at noon on sunny days (measured weekly by LI-250A; LI-COR Biosciences, USA).

2.3. Measurements

At the end of the experiment, for the treatments of no competition and with intra-genet competition, plants in each pot were harvested together. For the treatments of inter-genet competition, the two plants from the two genotypes in each pot were harvested separately. After we counted ramet number produced during the experiment, the plant was separated into leaves, stems and roots, dried at 70 °C for 72 h, and weighed. Total mass was calculated as the sum of aboveground mass (leaves and stems) and root mass. Root mass ratio was calculated as dry mass of roots divided by total dry mass. To measure competitive response, both for the intra-genet and inter-genet treatments, we calculated the log response ratio as LnRR = $\ln(B_i/B_0)$, where B_i is total mass or ramet number of replicate i (i = 1, 2,., 5) in a treatment with competition (intra-genet or inter-genet), and B_0 is the mean value of the variable across the five replicates in the corresponding treatment with no competition. Negative values of this ratio indicate competition and positive values indicate facilitation. More negative values of this ratio indicate a more negative effect of competition.

2.4. Data analysis

The data were analyzed in three steps. First, we tested whether the five genotypes differed in their ability to respond to temporal nutrient heterogeneity based on the data in the treatments with no competition. Two-way ANOVAs were used to test the effects of genotype (A, B, C, D, or E) and temporal nutrient heterogeneity (homogeneous vs. heterogeneous) on biomass (total mass, stem mass, root mass, and leaf mass), ramet number, and root mass ratio of *H. vulgaris*. Total, leaf, stem, and root mass and ramet number were
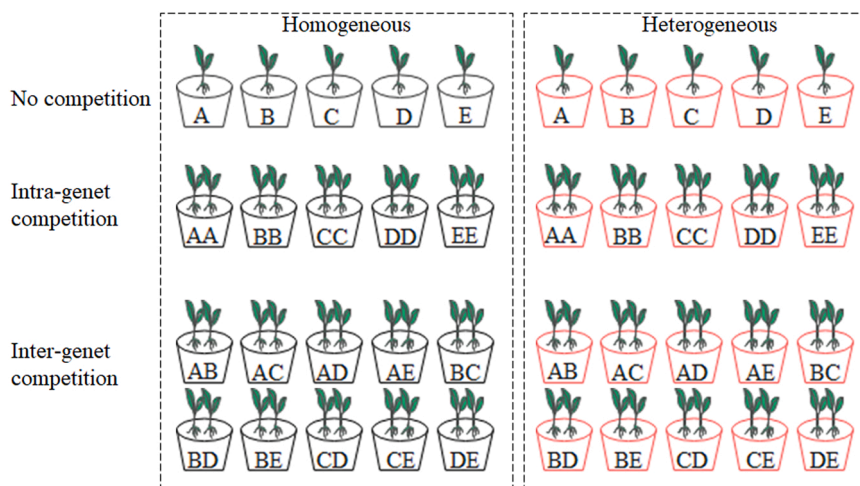

Fig. 1. The experimental design. One ramet (no competition), two ramets of the same genotype (intra-genet competition) or two ramets of different genotypes (inter-genet competition) of *H. vulgaris* were grown in a pot and supplied the pot with the same total amount of nutrients either homogeneously or heterogeneously. A-E represent the five different genotypes.

transformed to the natural log before analysis to improve homoscedasticity and normality. Following these ANOVA models, we carried out linear contrasts to test the differences between the homogenous and heterogeneous nutrient treatments for each genotype.

Second, we tested the effects of temporal nutrient heterogeneity on intra-genet competition. We used two-way ANOVAs to test the effects of genotype and temporal nutrient heterogeneity on intra-genet competitive response of *H. vulgaris*, measured as LnRR. Before analysis, values of all variables in the treatments with intra-genet competition were divided by the number of initial ramets (i.e., 2), so that the values were scaled to the level of per initial ramet and were comparable with no competition (Wang et al., 2014; Zhang et al., 2020).

Third, we tested the effects of temporal nutrient heterogeneity on inter-genet competition. We used three-way ANOVAs to test the effects of target genotype, competing genotype, and nutrient heterogeneity on inter-genet competitive response of *H. vulgaris*, measured as LnRR. When a genotype was considered the target genotype, all other four genotypes were each considered a competing genotype. For instance, if genotype A was considered the target genotype, then genotype B, C, D and E were each treated as a competing genotype. Similarly, when genotype B was treated as the target genotype, then genotype A, C, D and E were each considered a competition genotype. Statistical analyses were carried out with SPSS 19.0 (IBM, Armonk, NY, USA).
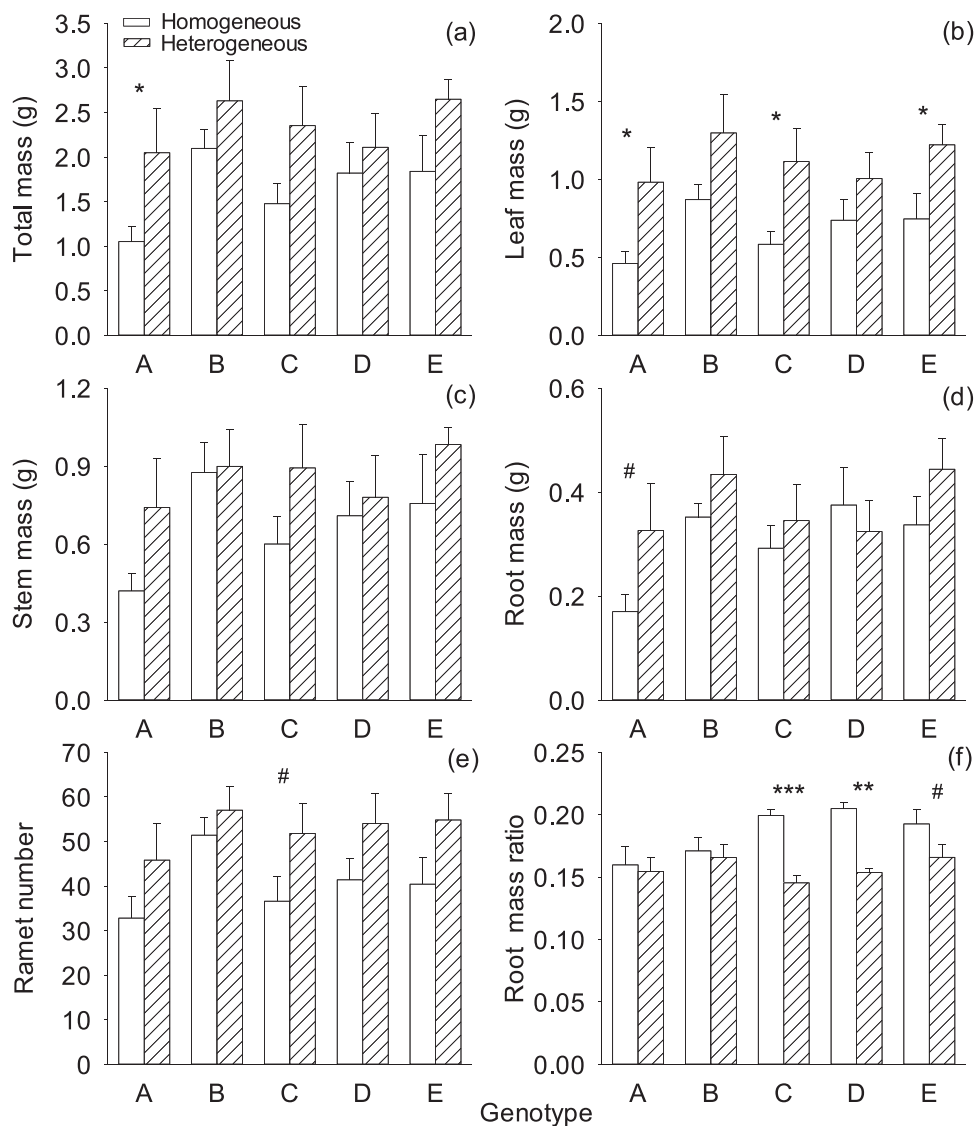

Fig. 2. (a-d) Biomass, (e) ramet number, and (f) root mass ratio of the five genotypes (A, B, C, D, and E) of *Hydrocotyle vulgaris* under homogeneous and heterogeneous nutrient supply with no competition. Values are mean + SE (n = 5). Symbols indicate the levels of differences between homogeneous and heterogeneous nutrient supply within a genotype (*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, and $^{\#}$ $0.05 < P < 0.1$).

3. Results

3.1. Growth response under no competition

Averaged across genotypes, heterogeneous (pulsed) nutrient supply increased total mass, leaf mass, and ramet number of *H. vulgaris* by 31.6–70.6% compared with homogeneous (continuous) nutrient supply (Fig. 2a, b, e; Table 1, $P < 0.01$). Considering individual genotypes, heterogeneous nutrient supply markedly increased total mass of genotype A, but had no significant effect on total mass of the other four genotypes (B, C, D, and E) compared with homogeneous nutrient supply (Fig. 2a). Heterogeneous nutrient supply also significantly increased leaf biomass of three genotypes (A, C and E), but had no significant effect on the other two genotypes (B, D; Fig. 2b). Root mass ratio was significantly or marginally significantly smaller in heterogeneous than in homogeneous nutrient supply in three genotypes (C, D, and E), but was not affected by the pattern of nutrient supply in the other two genotypes (A, B; Fig. 2f). These results suggest that the five genotypes differed in their responses to temporal soil nutrient heterogeneity.

3.2. Intra- and inter-genet competitive response under competition

Intra-genet competitive response, as measured by the log response ratio (LnRR) of total mass or number of ramets, did not differ between homogeneous and heterogeneous nutrient supply, and such an effect was independent of genotypes (Fig. 3, Table 2). The effect of temporal nutrient heterogeneity on inter-genet competitive response varied significantly depending on target genotypes (Fig. 4, Table 3). Temporal nutrient heterogeneity significantly decreased LnRR of total mass in one genotype (B), but had no effect on the other four genotypes (A, C, D, and E; Fig. 4a). Temporal nutrient heterogeneity significantly decreased LnRR of number of ramets in genotype B, but significantly increased that in genotype E (Fig. 4b).

4. Discussion

We found that heterogeneous (pulsed) nutrient supply generally benefited the growth and asexual reproduction of *H. vulgaris* compared with homogeneous (continuous) nutrient supply, as reported before (Jankju-Borzelabad and Griffiths, 2006; James and Richards, 2007; Maestre and Reynolds, 2007; Osone et al., 2014; Yuan et al., 2017). Plasticity (i.e. changes in the phenotypic expression of a genotype under different environmental conditions) significantly contributes to the ability of plants to cope with temporal and spatial environmental heterogeneity (Grime and Mackey, 2002; Valladares et al., 2007). Plants possess different strategies to adapt to fluctuating environments, and some species are highly effective at rapidly capturing resources, which benefit their growth under pulsed nutrient supply (Esque et al., 2010; Lu et al., 2016; Liu and van Kleunen, 2017). Additionally, connected ramets of clonal plants can share resources and thus may make better use of spatially and temporally heterogeneously distributed nutrients (Song et al., 2013; Chen et al., 2019; Roiloa et al., 2019; Estrada et al., 2020; Portela et al., 2021; Wang et al., 2021).

Temporal nutrient supply changed the growth and biomass allocation of some genotypes of *H. vulgaris*, but had no impact on those of other genotypes (Fig. 2). These results support our first hypothesis and suggest that genotypes of *H. vulgaris* can vary in their response to temporal nutrient heterogeneity. This is very likely because some genotypes could efficiently take up resources to facilitate plant growth when faced with relatively high resource periods, but other genotypes may not. These results provide direct evidence that plastic responses of plants to temporal resource heterogeneity can differ between genotypes within the same species. As temporal resource heterogeneity is common in natural habitats (James and Richards, 2005; Padilla et al., 2013; Wang et al., 2016; Yu et al., 2019; Slate et al., 2021), genetic differences in responses to temporal resource heterogeneity may potentially play an important role in structuring plant populations and further influencing their dynamics as it may alter intraspecific interactions. In a recent study, intra-population epigenetic variation of *H. vulgaris* was found to be related to its genetic variation (Wang et al., 2020). Thus, in this study, epigenetic differences might also be involved in the differences of the plastic responses of *H. vulgaris* to temporal resource heterogeneity. Further studies could test this novel hypothesis.

A reduction in proportional biomass allocated to roots detected in some genotypes (C, D, E) in response to temporal heterogeneity in nutrient supply fits with the optimal partitioning theory, which predicts an increase of the relative biomass allocated to structures that acquire the most limiting resource (Thornley, 1972; Bloom et al., 1985; Poorter and Nagel, 2000). In our study, nutrients added as a pulse triggered this response in several genotypes. Punctual addition of a greater concentration of nutrients decreased proportional biomass allocated to roots, in comparison with homogenous addition of nutrients, even when the total amount of nutrients added in both treatments was equal. This plastic response was not found in genotype A where we found a significant benefit of total biomass of

Table 1

ANOVAs for effects of genotype and temporal nutrient heterogeneity on biomass, ramet number, and root mass ratio of *Hydrocotyle vulgaris* in the treatments with no competition.

Effect	df	Total mass	Leaf mass	Stem mass	Root mass	Ramet number	Root mass ratio
Genotype (G)	4, 40	2.40[#]	2.22[#]	2.08 ns	**3.19***	1.98 ns	1.83 ns
Heterogeneity (H)	1, 40	**8.79****	**18.41*****	4.00[#]	2.48 ns	**8.94****	**22.13*****
G × H	4, 40	0.40 ns	0.33 ns	0.42 ns	0.72 ns	0.26 ns	**3.05***

Degrees of freedom (*df*), F-values and significance levels (*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, # $0.05 < P < 0.1$, and ns $P \geq 0.1$) are shown. Values are bold where $P < 0.05$.
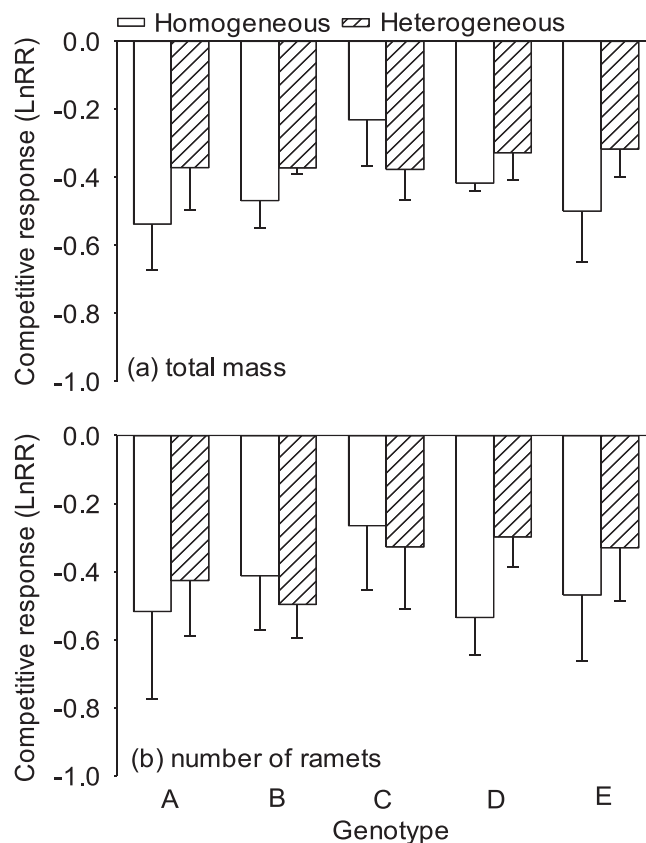
Fig. 3. Intra-genet competitive response, measured by log response ratio (LnRR) of (a) total mass and (b) number of ramets, of the five genotypes (A, B, C, D, and E) of *Hydrocotyle vulgaris* under homogeneous and heterogeneous nutrient supply. Values are mean + SE (n = 5).

Table 2
ANOVAs for effects of genotype and temporal nutrient heterogeneity on intra-genet competitive response of *Hydrocotyle vulgaris*, as measured by log response ratio (LnRR) of total mass and number of ramets.

Effect		LnRR of total mass		LnRR of number of ramets	
	df	*F*	*P*	*F*	*P*
Genotype (G)	4, 40	0.34	0.849	0.64	0.638
Heterogeneity (H)	1, 40	0.37	0.547	1.46	0.234
G × H	4, 40	0.33	0.853	0.84	0.507

Degrees of freedom (*df*), F and *P* values are given.

heterogeneous nutrient supply (i.e. nutrient pulse). A plausible reason for this result is that genotype A allocated a similar biomass to produce roots when nutrients were added homogeneously and heterogeneously. With this similar response, total biomass was significantly higher in the heterogeneous than in the homogeneous treatment.

Temporal nutrient heterogeneity had no impact on intra-genet competition of *H. vulgaris*, supporting the second hypothesis. This is likely because the ramets of *H. vulgaris* used for intra-genet competition were similar in size, morphology, developmental stage and vegetative generation, which responded similarly to temporal nutrient heterogeneity. Consequently, competition between these ramets could not be altered by temporal nutrient heterogeneity. In clonal plant populations, however, ramets of the same genotype can also differ greatly in size, morphology, developmental stage, and/or vegetative generation (Wang et al., 2014; Batzer et al., 2017; Adomako et al., 2021), which may influence their responses to temporal nutrient heterogeneity. If ramets of different sizes, morphologies, developmental stages or vegetative generations are under competition, then temporal nutrient heterogeneity may alter intra-genet competition even if they belong to the same genotype. Further studies should be conducted to test this hypothesis.

An additional explanation for the absence intra-genet competition found in our study is based on the potential capacity for self/non-self competition. It seems reasonable that natural selection will favor strategies to reduce competition within the same genotype (i.e. self-competition; Grosberg and Hart, 2000; Kimura and Simbolon, 2002). Thus, avoidance of competition between members of the same clone should be beneficial, with a positive feedback in terms of growth. In this line, avoidance of competition has been previously
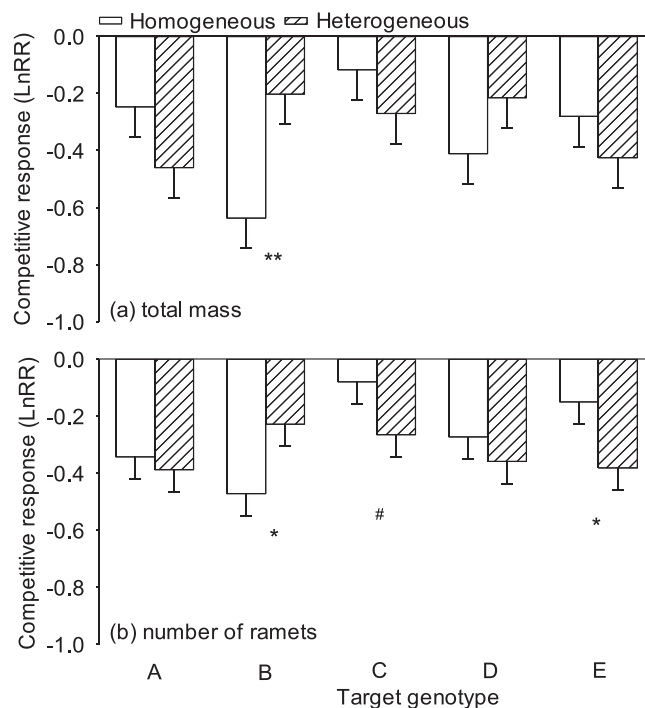
Fig. 4. Inter-genet competitive response, measured by log response ratio (LnRR) of (a) total mass and (b) number of ramets, of the five target genotypes (A, B, C, D, and E) of *Hydrocotyle vulgaris* under homogeneous and heterogeneous nutrient supply. Values are mean + SE. Symbols indicate the levels of differences between homogeneous and heterogeneous nutrient supply within a genotype (** $P < 0.01$, * $P < 0.05$, and # $0.05 < P < 0.1$).

Table 3
ANOVAs for effects of target genotype, competing genotype, and temporal nutrient heterogeneity on inter-genet competitive response of *Hydrocotyle vulgaris*, as measured by log response ratio (LnRR) of total mass and number of ramets.

Effect		LnRR of total mass		LnRR of number of ramets	
	df	*F*	*P*	*F*	*P*
Target genotype (T)	4, 160	1.00	0.408	1.30	0.273
Competing genotype (C)	4, 160	0.85	0.497	1.62	0.171
Heterogeneity (H)	1, 160	0.13	0.722	1.53	0.218
T × H	4, 160	**3.82**	**0.005**	**2.88**	**0.024**
T × C	11, 160	1.25	0.261	**1.92**	**0.040**
C × H	4, 160	0.41	0.799	0.09	0.985
T × C × H	11, 160	0.36	0.970	0.76	0.675

Degrees of freedom (*df*), F and P values are given. Values are bold where $P < 0.05$.

reported between roots of the same individual and between roots of genetically identical individuals, demonstrating the capacity for self/non-self recognition as a mechanism to avoid self-competition between individuals (ramets) of the same genotypes (Falik et al., 2003; Holzapfel and Alpert, 2003; Gruntman and Novoplansky, 2004; Schenk, 2006). In some cases, this self/non-self genotype recognition was mediated by physiological integration, with root cooperation only detected in the system of connected ramets (Holzapfel and Alpert, 2003; Roiloa et al., 2014). In our study, ramets of the same genotypes were disconnected, suggesting that physiological integration was not responsible for the absence of intra-genet competition.

Our results also support the third hypothesis that temporal nutrient heterogeneity can affect inter-genet competition of *H. vulgaris* when genotypes differ in their ability to respond to temporal nutrient heterogeneity. In our study, genotype A, even showing a significant growth increase in response to nutrient pulse (heterogeneous supply), produced the smallest total biomass compared with other genotypes. That is, although genotype A was the only genotype that experienced a significant increase in biomass in response to nutrient pulse, this benefit was not transferred to a competitive advantage when growing with other genotypes of the same species. On the contrary, genotype B, which did not experience a significant benefit in terms of total biomass from pulsed nutrient addition, did show a competitive advantage in this heterogeneous treatment. Additionally, we observed a competitive benefit (i.e. less negative effect of competition) of homogeneous nutrient addition for genotype C and E in terms of ramet number. This benefit is probably supported by the fact that both genotypes responded to homogeneous nutrient addition by significantly increasing the proportional

biomass allocated to roots, which could ameliorate the low efficiency of nutrient acquisition, and consequently increase new ramet production. Overall, these results reveal that the responses to heterogeneous nutrient supply observed at the level of individual genotypes cannot be directly extrapolated to the competitive responses at the population level. Thus, predictions over population dynamics are complex, as responses of genotypes can be quite different.

5. Conclusions

In conclusion, temporal heterogeneity in nutrient supply may increase the growth of clonal plants such as *H. vulgaris* but can have little effect on intra-genet competition, so that it may help clonal plants to compete with other species. Different genotypes of clonal plants may respond differently to temporal nutrient heterogeneity so that temporal nutrient heterogeneity may influence their intraspecific interactions by altering inter-genet competition. Studying how patterns of resources distribution, both at spatial and temporal scales, can differentially affect different genotypes of the same species is a key to understand effects of intraspecific diversity on population dynamics and structure. However, our study involved only one clonal species, and future studies could test the generality of our findings by studying a group of clonal plant species.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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