Pak. J. Bot., 49(4): 1491-1496, 2017.

THE ALLELOPATHIC POTENTIAL OF *OXALIS RUBRA* ON SEEDLINGS OF *VERONICA PERSICA* UNDER DIFFERENT ENVIRONMENTS

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Abstract

Allelopathy is an important ecological mechanism in nature, which is extensively investigated and acknowledged as an innate characteristic. Less is known how the direction and strength of allelopathy may change with different environments in living plants. We studied the allelopathic potential of *Oxalis rubra* on seedlings of *Veronica persica*, a cosmopolitan weed, planted under two environments (light incubator and laboratory) with fundamental difference in light intensity. In the light incubator, *O. rubra* showed a moderate level of inhibition on the leaf growth of *V. persica*, probably due to a higher concentration or faster release of allelochemicals owing to high resource availability. On the contrary, the presence of *O. rubra* played a significant role in promoting the survival of *V. persica* seedlings in the laboratory, likely ascribed to water retention by *O. rubra* plants or stimulatory allelopathy in the different environment. Our study contributes to empirical investigations on how allelopathy varies with different conditions and points out the importance of environmental heterogeneity on allelopathy.

Key words: Allelopathy, Context-dependent, *Oxalis rubra*,*Oxalis articulata*,*Veronica persica*.

Introduction

Allelopathy is the effect of a donor plant on a recipient plant through the release of chemical compounds into the surrounding environment (Levine *et al.*, 2003; Meiners, 2014; Da Silva *et al.*, 2015), which is vital for donor plants to improve their survival and competitive ability (Rivoal *et al.*, 2011; Meiners *et al.*, 2012; Dai *et al.*, 2016). The allelocompounds can have either stimulatory or inhibitory effects on recipient plants, varying with interacting species and/or concentrations of the chemicals (Meiners *et al.*, 2012; Butnariu *et al.*, 2015; Sayed *et al.*, 2016).

Extensive studies have shown that allelopathic effects can significantly inhibit physiological and ecological processes of recipient plants, such as survivorship (Nilsen *et al.*, 1999; Weidenhamer, 2006; Muzell Trezzi *et al.*, 2016), and growth of seedlings (Butnariu *et al.*, 2015; Tanveer *et al.*, 2015). Nevertheless, allelopathy can also promote survival or growth as well. For example, water extraction of rice root can significantly elevate the seedling growth of Lettuce (Ma *et al.*, 2014). However, allelopathy is not an isolated phenomenon in nature. Environment is largely heterogeneous across time and space, and hence it is often subjected to environmental variation (Chon & Nelson, 2013). Many factors (e.g. radiation, temperature, humidity, light) have been proved to alter allelopathic effects of the same plant pairs (Kobayashi, 2004; Pedrol *et al.*, 2006). Therefore, to study allelopathy of a donor plant on a recipient plant, the environment that connects the two should be taken into serious consideration (Blanco, 2007, Muzell Trezzi *et al*., 2016).

On one hand, the intensity of allelopathy may be affected by environmental factors (Lobón *et al.*, 2002; Chen *et al.*, 2012; Muzell Trezzi *et al.*, 2016). Previous studies have demonstrated that the allelopathic intensity of *Prymnesium parvum* could strengthen as temperature and light were elevated (Granéli & Salomon, 2010). On the other hand, the stress hypothesis of allelopathy stated that the direction of allelopathy could also change with abiotic variations (Pedrol *et al.*, 2006). For example, the allelopathy of *Microcystis aeruginosa* on algal blooms was totally different with different temperatures, which showed great promotion at low temperature (20ºC), but inhibition at high temperature (≥25ºC) (Ma *et al.*, 2015).

Oxalis rubra (Oxalidaceae) sometime treated as a subspecies of *O. articulata* (Lourteig, 2000) is a perennial herb widely, cultivated as an ornamental ground-covering plant in tropical, subtropical, and temperate regions (Liao *et al.*, 2015). Besides its characteristics of fast growth, long flowering period, and beautiful flowers, *O. rubra* also possesses inhibitory allelopathic effect on many other weeds (Shiraishi *et al.*, 2002; 2005), which can greatly reduce the application of chemical herbicides on horticultural and agricultural ecosystems and thus alleviate environmental concerns and sustain an eco-friendly landscape (Li *et al.*, 2010; Han *et al.*, 2013; Ma *et al.*, 2014; Jabran *et al.*, 2015; Shah *et al.*, 2016). *Veronica persica* (Scrophulariaceae), on the other hand, is a short-lived (annual or biennial) cosmopolitan weed, famous for its worldwide invasion and harmful influences on crops (Yin *et al.*, 2012; Wang *et al.*, 2013). *Oxalis rubra* and *Veronica persica* usually co-occur in gardens, lawns, and roadsides. However, field observations reveal that *O. rubra* is typically the dominant herb whereas *V. persica* and other weeds only grow along edges, highlighting the allelopathic potential of *O. rubra* in natural habitats. In addition, the wide environmental range of both species has set differential scenarios to study allelopathic effect, namely, the importance of context-dependent allelopathy (Bauer *et al.*, 2012; Ladwig *et al.*, 2012; Meiners *et al.*, 2012; Ma *et al.*, 2015).

This study aims to look into the allelopathic potential of *O. rubra* on the survival and growth of *V. persica* seedlings under two different environmental conditions, one in the light incubator with sufficient light (a mimic of open field or light gaps), and the other in the laboratory with limited light (a mimic of understory or shaded conditions). Such environmental difference is expected to result in varied levels of resource availability and thus alter resource allocation patterns in donor plants. Specifically, when the resource availability is low (e.g. limited light), the donor plant would save resources for its own growth and maintainance instead of investing in allelopathy (Herms & Mattson, 1992; Rivoal *et al*., 2011). Our hypotheses are that: 1, there is an overall inhibitory effect of *O. rubra* on the survival and growth of *V. persica* seedlings; and 2, the allelopathic effect on seedling survival and growth is weaker in the laboratory than the light incubator.

Materials and Methods

Collection of *Oxalis rubra* rhizomes and plant cultivation: Since *O. rubra* has been widely cultivated and escaped into natural habitats across China, we chose an abandoned field (a square of approximately 2500 m^2) grown with *O. rubra* at the campus of Hubei University, Wuhan, Hubei Province of China (30°34′46.37″N, 114°19′39.48″E). The belowground rhizomes (~2cm^3) of 40 plants were dug out using shovels and immediately transplanted into the middle of small pots (with diameter of 7.5cm, and depth of 5cm) in October of 2014. We intentionally avoided clone strains of *O. rubra* by sampling with at least 5-meter intervals. After 2 months of growth, most *O. rubra* rhizomes had survived, shoot out leaves and some even started to flower. The soil used to cultivate *O. rubra* was a mixture of collection from other bare sites around the campus and 30 additional pots with soil of the same origin and amount were prepared for the control treatment (namely without allelopathy, see *Experimental design*).

Seed collection and germination of *Veronica persica*: *Veronica persica* is a very common weed in gardens, lawns, and abandoned fields in China. In May 2013, around 50 ripe fruits of *V. persica* individuals (randomly picked, one fruit per individual) were collected across the campus of Hubei University. A total number of 767 seeds were kept in paper bags at 4ºC in a refrigerator. To germinate the seeds, 15 seeds were evenly spread onto a 10 cm petri dish with wet filter papers. Germination was carried out in a light incubator (QHX-250BS-III, Xinmiao, Shanghai) set at 15ºC and a 12-hour light/dark regime. Water was sprayed on seeds everyday and geminated seedlings were regarded as ready for transplant when the two cotyledons fully spread out.

Experimental design: There were two treatment groups in our experiment, namely an allelopathy group with *O. rubra* plants and a control group without them. Six seedlings of *V. persica* were transplanted and spaced evenly into the same peripheral locations in a pot with or without *O. rubra*. Prior to transplant, sufficient water was added to all pots. In the allelopathy group, the distance between *V. persica* seedlings and the central *O. rubra* was about 3 cm, which resembles typical natural densities.

Allelopathic effects were examined under two environments, one in the light incubator set at 20ºC and 12-hour of sufficient light, a mimic of open field or light gaps; and the other on the benches in the laboratory with 12-hour lighting as well, but, limited light intensity, a mimic of understory or shaded conditions. Such light difference is very common in natural habitats for both species. However, besides light, other physical factors such as humidity and temperature also co-varied in the 2 environments, all of which we have kept good record of using a PAR meter (MQ-200, Apogee, USA) and a regular thermohygrometer throughout the experiments. Watering regime (light spray on leaves and topsoil) was the same for both groups under the two environments. Since the seeds of *V. persica* germinated sequentially, three batches of transplant were conducted. The first 2 batches included 10 pots in each treatment; and the last batch only had 3 pots in each. Plants in the light incubator were composed of the first and third batch, resulting in 78 seedlings of *V. persica* in both allelopathy and control treatments, while the laboratory held the second batch, a total of 60 seedlings of *V. persica* in both treatments. The problem that ‘batch’ might confound with ‘environment’ should not be a serious concern given that the *Veronica* seeds were composed of 50-ish genotypes and the number of batches was far less. In addition, we have statistically tested the effect of ‘batch’ on transplant shock (see Results) and for the incubator seedlings comprising two batches in terms of survival ($F_{1,131}$ = 2.93, P = 0.09) and growth ($F_{1,117}$ = 0.02, P = 0.90), indicating that batch did not play a big role in seedling performance.

We examined all plants every day, noted alive/dead for each *V. persica* seedling, and counted the number of true leaves on living seedlings every five days for a month. Due to common transplant shock, we counted all dead seedlings in the first five days as transplant failures and did not include them in the following observation and analysis. Due to an unexpected air-conditioning failure at the end of the month, the temperature fluctuated largely in the laboratory. Therefore, we did not include the last measurement in the laboratory, resulting in five time points for light incubator plants and four time points for laboratory plants. Throughout the experiment, all plants of *O. rubra* grew well with at least six compound leaves under both environments.

Data analysis: Data were analyzed using SAS statistical software (SAS institute, Cary, NC, USA). Differences in temperature, relative humidity, and light intensity of the light incubator and laboratory were analyzed using Student’s-t test. The success rates of transplant were calculated for each treatment group after every batch of transplant and chi-square test (proc freq) was used to test whether there was difference in success rates between allelopathy and control group. Meanwhile, we tested if the transplant shock differed among three batches using generalized linear mixed model (proc glimmix) with a binary-distributed response variable (“alive/dead”), “batch” as fixed effects and “pot” nested within treatments as a random effect.

To analyze the allelopathic effects of *O. rubra* on seedlings of *V. persica*, the survivorship and number of true leaves in allelopathy and control group were compared using generalized linear mixed models, one model separated by survey time and the other as repeated measures. In both analyses, treatment group was included as the fixed effect and “pot” nested within treatments as a random effect, while survivorship was the binary-distributed response variable and number of true leaves the Poisson-distributed response variable. In the analysis of leaf growth in *V. persica*, we treated those dead plants as missing values so that the leaf counts were not the compound of survival and growth, both of which were independently evaluated. Finally, since our goal was to explore context-dependent allelopathy, data from two environments were combined and the treatment by environment interaction was analyzed in the repeated measures to comprehensively evaluate whether the relative performance of *V. persica* seedlings growing with *O. rubra* was affected by specific environments.

Results

Environmental differences and success rate of transplant: Besides light intensity, temperature and relative humidity differed significantly between the light incubator and laboratory (Table 1). Basically, light incubator was a much lighter, wetter, and had warmer environment than the laboratory, which was often regarded as better for plant growth.

Overall, the transplant of *V. persica* seedlings was successful, with survivorship after 5 days of transplant at 84.42%. In the first batch, the survivorship was 80% in allelopathy group, and 88.33% in the control. There was no significant difference in seedling survivorship between the two treatments ($X^2 = 1.56$, $P = 0.21$). The results were similar for the second and third batch (Second: allelopathy 78.33% vs. control 86.67%: $X^2 = 1.44$, $P = 0.23$; Third: allelopathy 83.33% vs. control 100%: $X^2 = 3.27$, $P = 0.07$), which ensured that transplant shock did not confound with allelopathic effects in the experiment. In addition, the transplant was equally successful across three batches ($F_{2,230} = 0.65$, $P = 0.52$), revealing no clear trend of seedling quality among sequential batches.

Effects of *Oxalis rubra* on the survival of *Veronica persica* seedlings: Overall, *O. rubra* had little effect on the survival of *V. persica* seedlings in the light incubator (Fig. 1, Table 2), which suggests that allelopathy of *O. rubra* was not evident. However, in the laboratory, the presence of *O.rubra* significantly increased the survival of *V. persica* seedlings (Fig. 2, Table 2) and this effect was very different from the light incubator environment (Table 2). For the three surveys, seedlings of *V. persica* always had a higher survivorship growing with *O. rubra* than without (10 days after transplant: $F_{1,18}$= 7.93, $P = 0.01$; 15 days after transplant: $F_{1,18} = 9.90$, $P = 0.006$; 20 days after transplant: $F_{1,18} = 16.20$, $P = 0.0008$; Fig. 2). Over the whole observation period, the survivorship of *V. persica* seedlings showed a significant downward trend (Figs. 1 & 2), and this trend was similar between two treatments (Table 2), indicating seedling loss or strong early selection against low-quality seedlings through the first month of growth.

Effects of *Oxalis rubra* on the growth of *Veronica persica* seedlings: In the light incubator, although there was no overall significant allelopathic effect on growth (Table 2), the number of true leaves on the seedlings of *V. persica* tended to be higher in the control than allelopathy group (Fig. 3). Especially, this reached a significant difference after 15 days of transplant ($F_{1,21} = 4.81$, P= 0.04), indicating that the presence of *O. rubra* might have some inhibitory effect on the growth of *V. persica* seedlings. Whereas in the laboratory, *O. rubra* had no significant impact on the number of true leaves on *V. persica* seedlings (Fig. 4, Table 2). Nonetheless, the effect of *O. rubra* on seedling growth was not significantly different between two environments (Table 2). During the entire observation period, the number of true leaves gradually increased over time (Figs. 3 & 4) and this growing trend was similar between two treatments (Table 2), suggesting comparable growth rates of *V. persica* in both treatments.

Table 1. The comparison of physical factors (mean ±s.e.) in the light incubator and laboratory.

Physical factors	Temperature (ºC)	Relative humidity (%)	Light intensity (μmol•m^{-2}•s^{-1})
Light incubator	19.30 ± 0.31	57.50 ± 1.67	7.60 ± 0.12
Laboratory	17.15 ± 0.38	34.50 ± 2.16	1.10 ± 0.06
Student’s t	4.38	8.44	43.42
P	0.0014	＜0.0001	＜0.0001

Table 2. Results of a generalized linear mixed model of the effects of treatment (allelopathy vs. control), time, and environment in the light incubator and laboratory, separately and combined, on the survival and growth of *Veronica persica* seedlings.

Dependent variable Source	Survival						Growth					
	Light incubator			Laboratory			Light incubator			Laboratory		
	df	*F*	*P*	df	*F*	*P*	df	*F*	*P*	df	*F*	*P*
Treatment	1,132	0.53	0.47	1,18	15.88	0.0009	1,118	2.65	0.11	1,18	0.97	0.34
Time	3,396	23.44	<0.0001	2,273	12.65	<0.0001	3,221	13.85	<0.0001	2,171	8.4	0.0003
Treatment × time	3,396	0.62	0.60	2,273	0.78	0.46	3,221	2.28	0.08	2,171	1.03	0.36

	Survival Combined			Growth Combined		
	df	*F*	*P*	df	*F*	*P*
Treatment	1,229	17.25	< 0.0001	1,198	3.23	0.07
Environment	1,229	0.19	0.67	1,198	9.44	0.002
Treatment × environment	1,229	10.99	0.001	1,198	0.31	0.58

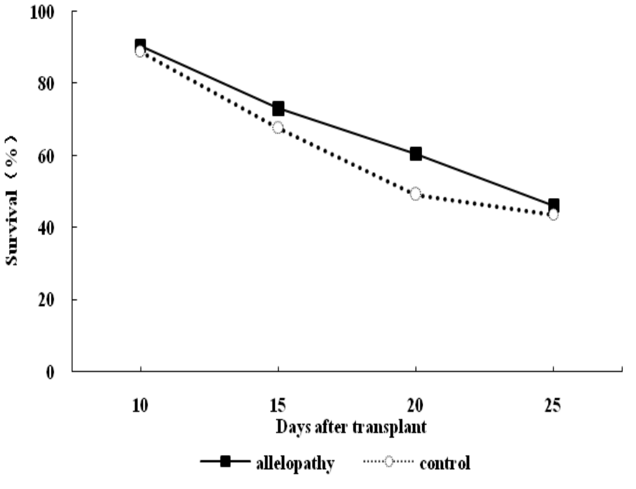

Fig. 1. The survivorship of *Veronica persica* seedlings in the allelopathy and the control group under the light incubator environment.

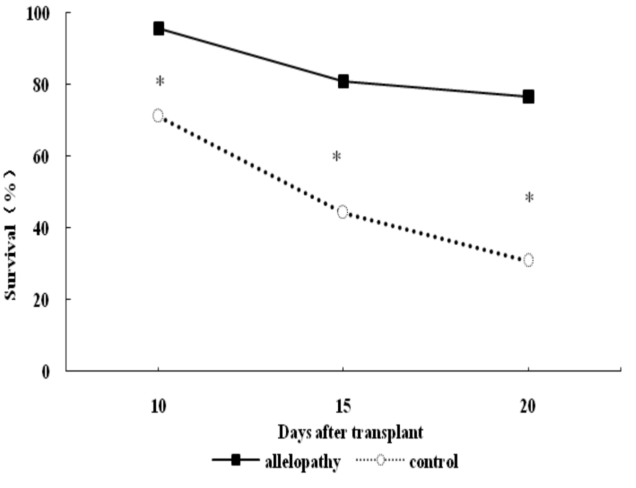

Fig. 2. The survivorship of *Veronica persica* seedlings in the allelopathy and the control group under the laboratory environment. *Indicates p<0.05.

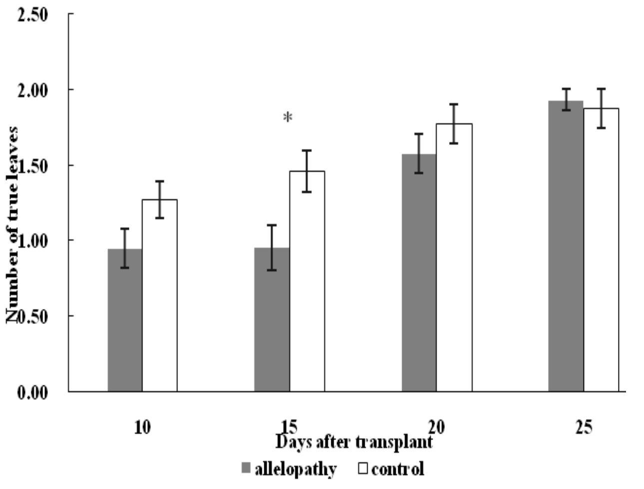

Fig. 3. The number of true leaves on *Veronica persica* seedlings in the allelopathy and the control group under the light incubator environment. *Indicates p<0.05.

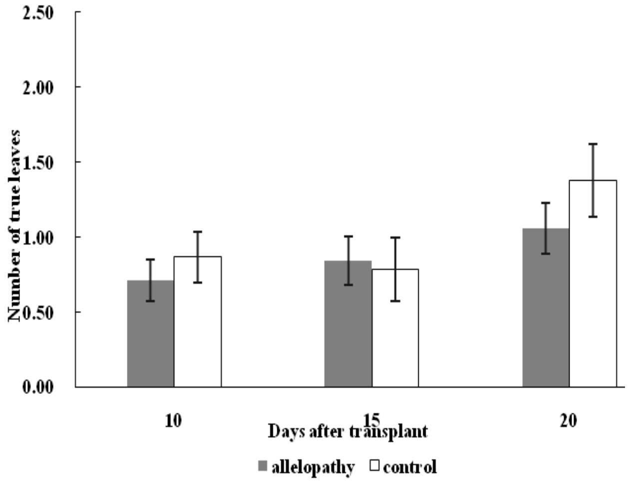

Fig. 4. The number of true leaves on *Veronica persica* seedlings in the allelopathy and the control group under the laboratory environment.

Discussion

Compared with the light incubator where little effect was observed, the existence of *Oxalis rubra* in the laboratory had a positive effect on the survival of *Veronica persica* seedlings. This contradicts with our hypothesis as we expected an overall inhibitory allelopathy. Considering the physical differences between the two environments, the laboratory was of limited light, low temperature and humidity (Table 1). Any factor that can alleviate such stress might help increase the survival of *V. persica,* for instance, more light, heat or water. In addition, it is well acknowledged that seedling growth requires good water availability(Hernández *et al.*, 2010; Roundy *et al.*, 2014).The existence of *O. rubra* might be especially useful in holding water from evaporation, which might increase the topsoil moisture contents for the shallow roots of the seedlings of *V. persica* to acquire. Another possibility is that the positive effect was a change in the direction of allelopathy induced by some allelochemicals from *O. rubra*. Although not investigated in this species, other studies have shown that when released in low concentrations and/or under lower temperatures, the allelochemicals of *Parthenium hysterophorus* and *Prorocentrum donghaiense* had positive effects on the survival or growth of other species (Shen *et al.*, 2015; Tanveer *et al.*, 2015).

The seedlings of *V. persica* tended to show an inhibitory response in leaf growth with the presence of *O. rubra* in the light incubator. This negative impact is likely an allelopathic effect of *O. rubra* on seedlings of *V. persica*, aiming at suppressing the growth of plants next to them, thus decreasing interspecific competition for resources and increasing the survival and growth of themselves (Rivoal *et al.*, 2011; Viard-Crétat *et al.*, 2012). Due to limited observational period, the growth of *O. rubra* was not strong, and plants in the light incubator only had about one more leaf than those in the laboratory (Luo WJ, personal observation), which implied that shading should not play a big role in inhibiting leaf growth of *V. persica* in the light incubator, where lights also came from lateral directions.

The absence of the inhibitory allelopathy on leaf growth in the laboratory was probably due to the reduction in the synthesis and/or release of certain allelochemicals, which is in agreement with our hypothesis. In the environment with low resource availability, secondary metabolism such as allelopathy may be balanced by the primary growth and maintenance of *O. rubra* plants (Herms & Mattson, 1992). Studies have shown that the strength of allelopathy in *Ipomoea cairica* and *Centaurea stoebe* decreased with light intensity and temperature (Tharayil & Triebwasser, 2010; Wang *et al.*, 2011; Chen *et al.*, 2012), the same direction as our results. However, the allelopathic effect on seedling growth was not as strong as expected in both the light incubator and the laboratory. We might be constrained in detecting such effect only based on leaf counts because there was limited growth in terms of the number of true leaves, especially in the harsh condition (e.g. most seedlings had 0 or 1; Fig. 4). Fresh weight or dry weight might be useful indices with a continuous distribution in evaluating allelopathy in future studies (Da Silva *et al.*, 2015). It is noteworthy that the allelopathic effect on the growth of seedlings was independent from that on survival. Thus there was a trend of seedling loss across the observational period, however, for the living seedlings, the trend of growth was obvious as well.

Regarding the debates on allelopathy and competition (Fuerst & Putnam, 1983; Nilsson, 1994; Del Moral, 1997), it is indeed not possible to separate them apart in our study. However, several lines of argument make allelopathy a more likely mechanism in explaining the differential responses than resource competition between *O. rubra* and seedlings of *V. persica*. First, the genus *Oxalis* is well known for its high concentration of oxalic acid (or oxalate), considered as fundamental allelochemicals in *Oxalis* plants (Shiraishi *et al*., 2005 and references therein). It has also shown that several species of *Oxalis* have strong allelopathic activity on various cosmopolitan weeds (Shiraishi *et al.*, 2002; 2005). Second, the environmental conditions in the light incubator were superior and there should not be depletion of resources, which is regarded as a key element of competition (Fuerst & Putnam, 1983). Thirdly, compared with the plants of *O. rubra*, the seedlings of *V. persica* were very small (only 1-2 true leaves) and the roots of those were shallow and tiny as well. There seems no competitive interference between the two species above- or below- ground. Therefore, the effect of *O. rubra* on seedlings of *V. persica* in our study is probably attributed to allelopathy through natural release of chemicals, which appears an inherent property of *Oxalis* plants.

Overall, our results revealed that the allelopathic effects of *O. rubra* on seedlings of *V. persica* were different between two environments. In the light incubator, there was a moderate level of inhibition on growth of *V. persica*, but not strong enough to further affect survival. In the laboratory, the inhibitory effect was not observed, which might be a manifestation of weakened allelopathy of *O. rubra* in response to low resource availability in inferior conditions. Moreover, stimulation on survival of *V. persica* seedling was significant in the laboratory, indicating an overriding effect of water retention or a change in the direction of allelopathy. Such context-dependent allelopathy has also been found in some species pairs (Lobón *et al.*, 2002; Shen *et al.*, 2015) or with different allelochemicals (Einhellig, 1996; Muzell Trezzi *et al.*, 2016). It suggests that allelopathy should not be regarded as a steady effect; however, the heterogeneity of environmental conditions should be noted and measured in studies of allelopathy (Bauer *et al.*, 2012; Meiners *et al.*, 2012). Still, it is not clear whether the change in strength and/or direction of allelopathy is due to the same allelochemicals or different reactions, if other physical influences are involved such as shading, water retention or physical support, and whether there are physiological modifications in the recipient plants confounding with allelopathy, the answers to which await more experimental studies.

Acknowledgements

We are grateful to Xue Yang for her hard work in the field and the laboratory. We thank Department of Biology at University of Virginia for statistical assistance,Lu Miao, Lena Li, and Yu-ting Weng for their comments on the manuscript. This work was funded by the National Natural Science Foundation of China to Can Dai (31270279), Kuo Liao (31200170), and Zheng-Xiang Wang (41471041).

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(Received for publication 10 June 2016)