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Fast seedling root growth leads to competitive superiority of invasive plants

Ming Ni · Yu Liu · Chengjin Chu · Han Xu · Suqin Fang

Abstract The competitive superiority of invasive plants plays a key role in the process of plant invasions, enabling invasive plants to overcome the resistance of local plant communities. Fast aboveground growth and high densities lead to the competitive superiority of invasive species in the competition for light. However, little is understood of the role belowground root competition may play in invasion. We conducted an experiment to test the effect of root growth on the performance of an invasive shrub *Cassia alata*, a naturalized, non-invasive shrub *Corchorus capsularis*, and a native shrub *Desmodium reticulatum*. We compared seedling growth of the three species and their competitive ability in situ. The roots of the *C. alata* seedlings grew much faster than those of *C. capsularis* and *D. reticulatum* during the entire growth period although *C. alata* had shorter shoots than *D. reticulatum*. Furthermore, *C. alata* showed an apparent competition advantage compared to the other two species as evidenced by less biomass reduction in intraspecific competition and higher competitive effects in interspecific competition. Our study reveals that fast seedling root growth may be important in explaining the competitive advantages of invasive plants. Future studies should pay more attention to the belowground traits of invasive plants, the trade-off between shoot and root growth, and the role of root competition in affecting the population dynamics of invasive plants and the structures of invaded communities.

Keywords Belowground · Biological invasion · Invasive plant · Root trait · Root competition

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Introduction

Invasive species have severe impacts on the biodiversity and functions of invaded communities (Mack et al. 2000; van Kleunen et al. 2015). A major focus of

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invasive studies is to understand the mechanisms of biological invasion and to identify factors determining plant invasiveness (Cadotte et al. 2006; van Kleunen et al. 2010). Competitive superiority has long been hypothesized to play a key role in the process of plant invasions (Levine et al. 2004). At the establishment stage, exotic plants face resistance from native plants, but superior competitive ability enables newly invading plants to overcome this resistance (Burke and Grime 1996; Amsberry et al. 2000). At the spreading stage, competitive ability determines the dominance and severity of invasive plants, and the invasive plants can exclude native species through intense interspecific competition (Simberloff et al. 2013).

Although many experiments have compared the competitive ability of native and invasive plants, and most results find that invasive plants are more competitive (Vilà and Weiner 2004), we still do not fully understand what lead to this competitive superiority (Gioria and Osborne 2014). Some researchers have pointed out that competitive superiority is caused by the fast growth of invasive plants (van Kleunen et al. 2010), and that individual size plays a key role in determining competitive ability (Keddy and Shipley 1989). For example, Morris et al. (2002) showed that invasive shrub *Ligustrum sinense* had a greater stem elongation and better light-capturing ability than the native shrub *Forestiera ligustrina*, leading the former to outcompete the native shrub in the field. Comparative studies between invasive plants and native plants have shown that invasive plants usually have a larger individual size, higher relative growth rate, and greater maximum height than native plants (Baker 1964; Grotkopp et al. 2002; Grotkopp and Rejmánek 2007; Leishman et al. 2007). Competitor density is also important (Silvertown and Charlesworth 2009; Iponga et al. 2008) as invasive plants may increase their competitive advantage by maintaining a high density (Levine 2008; Gioria and Osborne 2014). During the outbreak spreading stage of invasion, the great fecundity of invasive plants intensifies interspecific competition and consequently suppresses native species (Violle et al. 2009).

Plants compete through aboveground (i.e., shoots) for light and belowground (i.e., roots) for nutrients and water, but their actions are not always synchronous (Wilson 1988). Previous competition studies on invasive plants mainly focused on aboveground traits (Vilà et al. 2003; Ordonez and Olff 2013; Gioria and Osborne 2014). Only a few studies have investigated belowground traits (e.g., Liu and van Kleunen 2017), largely because of lack of suitable techniques (Schenk 2006; Kueffer et al. 2007; Dehlin et al. 2008). Some studies have revealed that roots play a key role in plant competition, community assembly, and diversity maintenance (Schenk 2006; Bardgett et al. 2014). Wilson (1988) summarized 23 studies, and found that most (68%) of them indicated that root competition had a larger negative effect than shoot competition on plant growth. Coomes and Grubb (1998) showed that removing root competition by trenching promoted the aboveground growth rates of both saplings and seedlings in an Amazonian caatinga. Root competition can be especially important at the seedling stage, because at first seedlings generally prefer root growth to acquire water and physical support (Dunbabin et al. 2013). Small differences in the initial sizes and growth rates of neighboring seedlings can result in different competitive abilities (Weiner 1990), particularly under conditions of high seedling density (Craine et al. 2005). Despite these advances, little is understood of root growth of invasive plants and belowground competition among invasive conspecifics and between invasive and native species.

This work addresses the following questions. Are exotic plant seedlings with rapid root growth more competitive than native plants in interspecific competition? Does rapid root growth of invasive plants intensify intraspecific competition of conspecifics? How does individual density affect root competition? To answer these questions, we conducted an experiment that consisted of the invasive shrub *Cassia alata* (Leguminosae), native shrub *Desmodium reticulatum* (Leguminosae), and naturalized, non-invasive shrub *Corchorus capsularis* (Tiliaceae) in a three-dimensional (3D) transparent growth system (Fang et al. 2009) to observe their seedling growth and competition in situ. We set two density levels and evaluated the responses of the three species in intraspecific and interspecific competitions. Our results infer that root growth may be important in determining the competition superiority of invasive plants.

Materials and methods

Materials and treatment

The three studied species (invasive *C. alata*, naturalized, non-invasive *C. capsularis*, and native *D. reticulatum*) involved in this study were from Heishiding Natural Reserve (N23.27°, E11.15°, Guangdong province, China). They all grow in the same habitat on roadsides or in abandoned fields. Native to South America, *C. alata* was first reported in China in 1934 (according to specimen records, www.nsii.org.cn). It has become a widespread invasive perennial shrub in South China (and is also a common invasive species in many tropical areas, Flora of China Editorial Committee 1994; Xu and Qiang 2011). Several researchers have reported its invasiveness, but few have investigated the mechanisms (Li et al. 2009; Yang 2011). *C. capsularis* was introduced from tropical Asia to China in 1910 as a commercial crop used as a fiber source. It is mainly planted in farmland, and it is considered as a naturalized, non-invasive plant (Flora of China Editorial Committee, 1994). The native shrub *D. reticulatum* is distributed in South China and Southeast Asia. Seeds of the three species were collected from Heishiding Nature Reserve in January 2015.

Before planting, seeds were surface-sterilized with hydrogen peroxide (20%) for 1 h and rinsed three times with sterile water. The sterilized seeds were germinated in the dark at 30 °C. Our pre-experiments recorded the germination time of the three species. Then in the formal experiment, we adjusted the germination time to make the seeds of the three different species germinate on the same day, and we only selected the seedlings with about 1 cm tap roots. Thus, the initial sizes and ages of the seedlings of the three species at planting are the same. The seedlings were transplanted to a 3D transparent growth system in growth chambers at 30 °C during the day and 25 °C at night on the same day. The 3D transparent growth system makes it possible to directly observe root growth (Fang et al. 2009). Different from the soil or sand based growth systems (Clark et al. 2011), ours allows 3D observation and measures of root growth. The growth cylinder is 20 cm in height and 10 cm in diameter, and it is filled with transparent growth medium, which consists of half-strength Hoagland solution and 0.2% Phytagel™ (Sigma-Aldrich, German).

Experimental design

To compare the competitive ability of the three species and detect the individual density effect, we set up a partial additive design (Goldberg 1990) with 18 combinations to test intraspecific and interspecific competitions (Table 1). For single growth without competitor, one individual of each species was grown in the cylinder alone. For intraspecific competition, one individual (phytometer) from each species was planted together with one or two conspecific individuals (competitor) in one cylinder (e.g. A-A or A-A-A). For interspecific competition, one individual (phytometer) was planted with one or two individuals of another species in one cylinder (e.g. A-B or A-B-B). For the intraspecific and interspecific planting, the distance between all individuals was 2 cm, which allowed the roots from neighboring plants overlapping even in the first week after transplanting. All the 18 combinations were grown for 3 weeks with six replicates.

Trait measurement

Plants were imaged in situ by camera (Nikon D600, EFS 60 mm, Japan) at days 7, 14, and 21 after germination. ImageJ software (version 1.49, National Institutes of Health, the USA) was used to measure the taproot length (cm) and shoot height (cm) based on the images. All plants were harvested at day 21 when root systems fully occupied the growth cylinder. The root traits, including total root length (cm), root volume (cm^3), number of lateral roots, root surface area (cm^2), and average root diameter (cm) were measured by WinRHIZO (Pro 2013a, Regent Instrument Inc., Canada). The shoot and root dry biomasses (mg) were measured after drying in an oven at 70 °C for 48 h. Specific root length was obtained dividing root length by root dry biomass. The root:shoot ratio was obtained dividing root dry biomass by shoot weight.

Data analysis

For the single planting, we used one-way ANOVA and Tukey's honest significant difference (HSD) multiple comparison method to compare the plant growth differences among the three species.

For the competition experiment, to assess whether the three species responded differently in intraspecific

Table 1 Experimental design with 18 species combinations. A, B, and C represent the three different species

Phytometer	Competitor(s)						
	No	A	B	C	A-A	B-B	C-C
A	Single	A-A	***A-B***	***A-C***	A-A-A	A-B-B	A-C-C
B	Single	***B-A***	B-B	***B-C***	B-A-A	B-B-B	B-C-C
C	Single	***C-A***	***C-B***	C-C	C-A-A	C-B-B	C-C-C

Because phytometer is taken as competitor in one-competitor interspecific competitions ("A-B" is the same as "B-A", bold and italic in table), there are totally 18 planting combinations in the experiment

and interspecific competition conditions, and whether competitor density influenced competition effects, we used three-way ANOVA to detect the phytometer identity, competitor identity and competitor density effects on the total biomass reductions (%) of phytometers in each combination. Here, the total biomass reduction (%) of a phytometer (compared to average total biomass in a single planting) represents the phytometer's fitness response.

We also assessed how plant root growth responded to competition. Three-way ANOVA were used to investigate phytometer identity, competitor identity and density effects on taproot length at different growth stages. To assess the responses of phytometers (except for biomass) to competition, we used mixed linear model (competitor identity and density as random factors) to analyze the relationship between the above mentioned traits of phytometers and competitor total root length (the total root length of neighboring competitors in one cylinder). The highly correlated traits were removed and only root:shoot ratio, root length, root average diameter, specific root length, and shoot height were used in the analysis.

All the calculations were run on R software (v3.1.1, The R Foundation for Statistical Computing).

Results

### Traits comparison for the three single plantings

Cassia alata had significantly longer taproots than those of the other two species in all three imaging periods (days 7, 14, and 21 after germination), but there was no apparent difference between *D. reticulatum* and *C. capsularis* over time (Fig. 1a). The three species had similar shoot heights at days 7 and 14, but
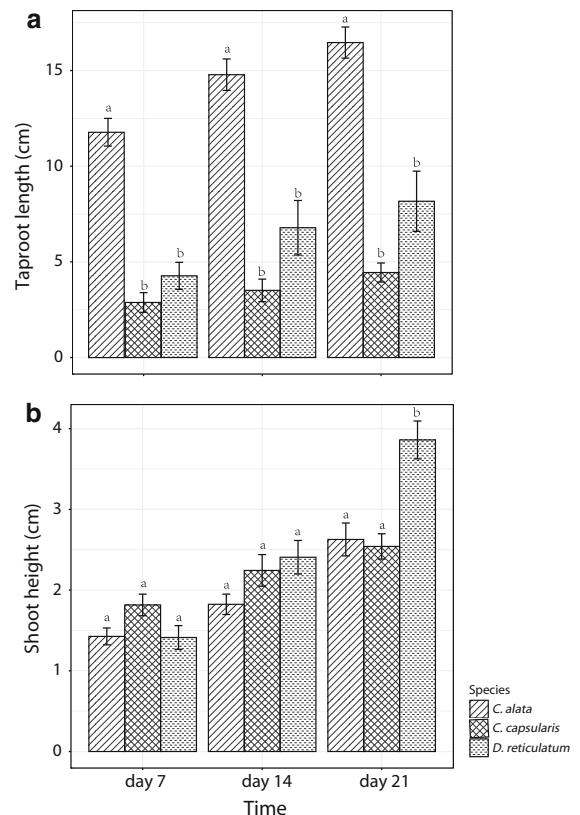
Fig. 1 The taproot length (**a**) and shoot height (**b**) of the three species on days 7, 14, and 21 after germination. Error bars represent standard error. Different bar annotations indicate significant differences ($p < 0.05$), and the same bar annotation indicates no significant difference ($p > 0.05$)

D. reticulatum had significantly longer shoots than the other two species on day 21 ($p < 0.001$, Fig. 1b).

Figure 2a and b show that *C. alata* had significantly larger total biomass and shoot biomass than *D. reticulatum* and *C. capsularis* on day 21, while no significant difference between the latter two species
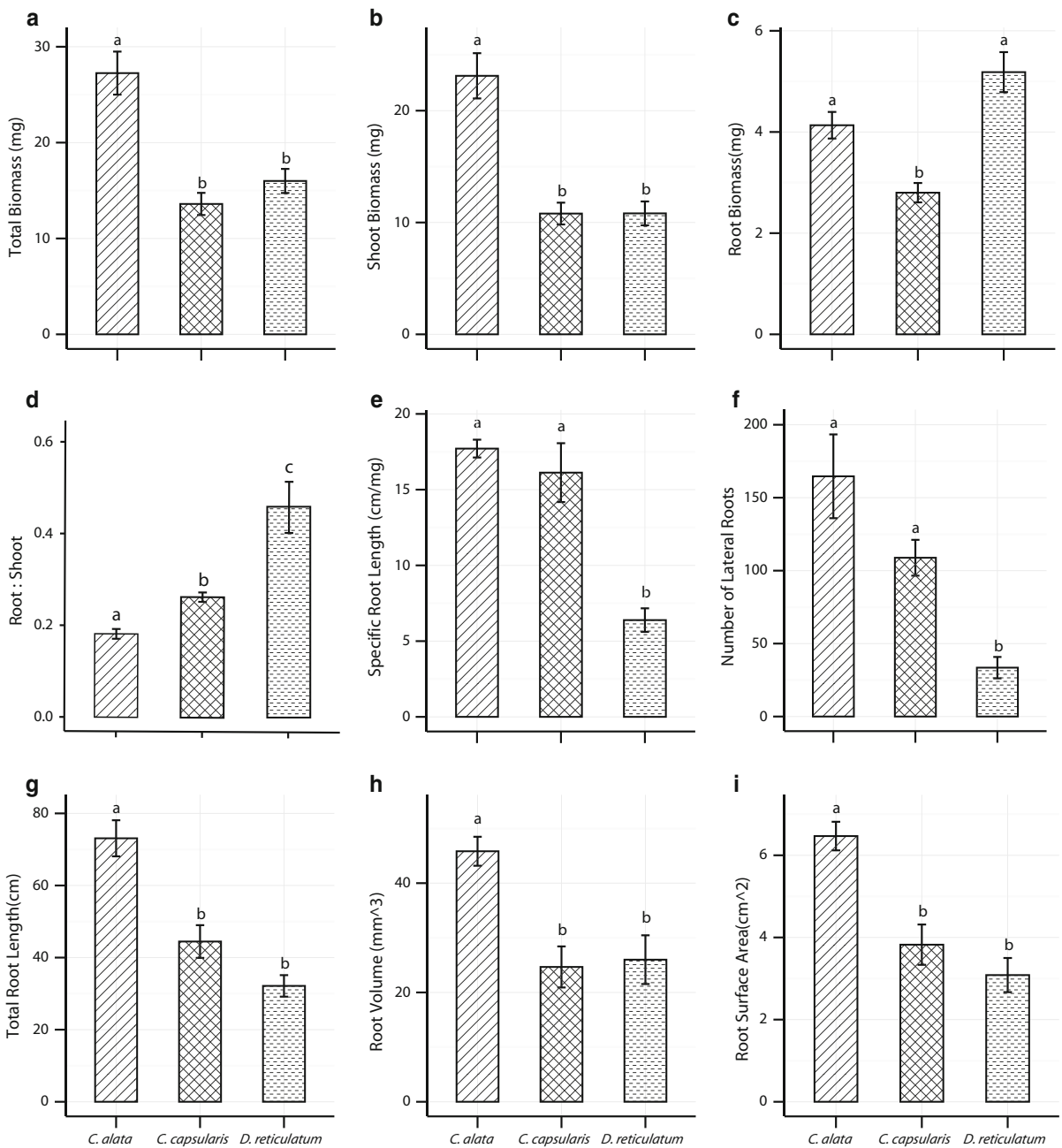
Fig. 2 Comparison of root traits of the three species on day 21. Different bar annotations indicate significant differences ($p < 0.05$), and same bar annotation indicates no significant difference ($p > 0.05$)

was observed. There was no significant difference in root biomass between *C. alata* and *D. reticulatum* (Fig. 2c), both of which had significantly greater root biomass than *C. capsularis*. The three species had significantly different biomass allocation patterns. *C. alata* had the least root:shoot ratio, and *D. reticulatum*

allocated more resources to roots (Fig. 2d). *C. capsularis* and *C. alata* had similar specific root length and number of lateral roots, both of which were significantly higher than those of *D. reticulatum* (Fig. 2e, f). *C. alata* had significantly larger total root length, root volume, and root surface area than *C. capsularis* and

D. reticulatum, while no difference between the latter two species in these three traits was observed (Fig. 2g–i).

Competition with conspecific and heterospecific neighbors

All the phytometer identity, competitor identity and density had significant effects on the biomass reduction of phytometers (Table 2). In intraspecific competition, the three species had similar biomass reductions under low competition density. However, under high competition density, *C. alata* had significantly less biomass reduction than *D. reticulatum*, but the difference with *C. capsularis* was not significant. Increasing competition density intensified plant biomass reduction, but the effect was only significant for *D. reticulatum* (Fig. 3a).

In interspecific competition, *C. alata* did not have any significant biomass change when competing with *D. reticulatum* or *C. capsularis* under both low and high competitor density (Fig. 3b, c, Online Resource 1, Fig. A1).

However, *D. reticulatum* and *C. capsularis* had significantly larger biomass reduction when competing with *C. alata*, and increasing competitor density intensified the competition response of *C. capsularis* (Fig. 3b, c). When *D. reticulatum* competed with *C. capsularis*, they had similar biomass reductions, and their competitive responses were intensified when competitor density increased (Fig. 3d, Online Resource 1, Fig. A1).

Taproot length dynamics and responses to competition

The taproots of *C. alata* were significantly shorter in competition with intraspecific and interspecific neighbors than those in single planting over the three periods from days 7 to 21 after germination ($p < 0.05$), except in competition with one individual of *C. alata* (Fig. 4a). The taproot length of *C. capsularis* was similar in most competition conditions (Fig. 4b), but it was significantly reduced in competition with two individuals of *C. alata* at day 21 ($p < 0.01$). *D. reticulatum* reduced its taproot growth in competition, but the reduction was significant only when grown with *C. alata* (Fig. 4c).

Neither the root:shoot ratio nor total root length of phytometers was significantly correlated with competitor total root length (Fig. 5a, c). The specific root length of *C. alata* was significantly reduced with the increase of competitor total root length. However, for *D. reticulatum* and *C. capsularis*, there were no significant relationships between phytometer specific root length and competitor total root length (Fig. 5b). *D. reticulatum* had significantly decreased shoot height with the increase in competitor total root length (Fig. 5d). Furthermore, the average root diameter of *C. capsularis* was significantly reduced with the increase of competitor total root length (Fig. 5e), but for *D. reticulatum* and *C. capsularis* there were no significant relationships between the above two traits.

Discussion

Our study provides evidence that invasive *C. alata* seedlings suppress native and naturalized, non-invasive plants possibly through rapid root growth in

Table 2 Analysis of variance for the effects of phytometer identity, competitor density and competitor identity on the total biomass reduction of phytometers

Effect	Sum Sq	Df	F value	Pr(> F)
Phytometer	7.015	2	160.232	**< 0.001**
Competitor	3.209	2	73.334	**< 0.001**
Density	0.738	1	33.347	**< 0.001**
Phytometer × competitor	0.360	4	4.119	**0.004**
Phytometer × density	0.230	2	5.267	**< 0.001**
Competitor × density	0.058	2	1.327	0.270
Phytometer × competitor × density	0.408	4	5.437	**0.002**
Residuals	1.969	90		

Significant effects ($p < 0.05$) are shown in bold
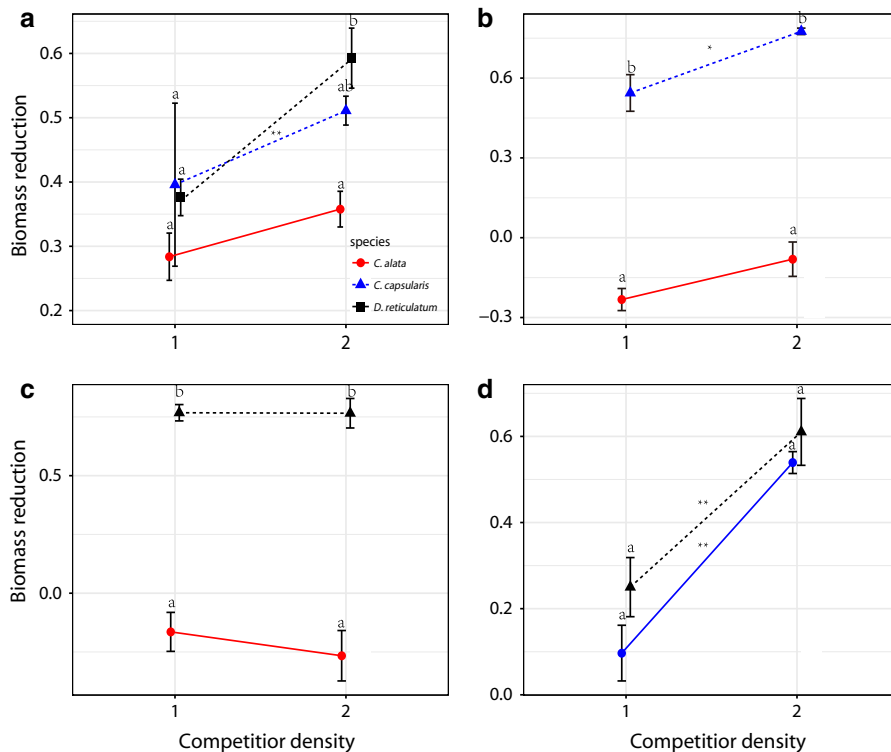
Fig. 3 Intraspecific competitions and interspecific competitions of the three species at day 21. **a** Intraspecific competitions; **b** *C. alata* competes with *C. capsularis*; **c** *C. alata* competes with *D. reticulatum*. **d** *C. capsularis* competes with *D. reticulatum*. The points represent phytometer biomass reduction in competition compared to single planting. The line annotation

* indicates the different levels between different competition intensity, with * meaning $p < 0.05$, ** meaning $p < 0.01$, and no annotation meaning no significant difference. The verbal annotation (abc) is the comparison between species under the same competitor density, with different verbal annotation meaning significant interspecific difference ($p < 0.05$)

competition. *C. alata* showed much more rapid taproot growth and larger root size (total root length, the number of lateral roots and root surface area) than those of the naturalized, non-invasive *C. capsularis* and native *D. reticulatum* without shoot height advantages. *C. alata* was more competitive than *C. capsularis* and *D. reticulatum*. The competitive superiority of invasive *C. alata* included less biomass reduction in intraspecific competition under high competitor density compared to those of the other two species, and significant interspecific competitive advantages. On the contrary, naturalized, non-invasive *C. capsularis* had similar taproot growth and final root size with native *D. reticulatum*. Furthermore, *C. capsularis* and *D. reticulatum* had similar performances in both intraspecific and interspecific competitions. Competitor density increased the competitive effects in some scenarios, especially when the competition effects were relatively low.

Root growth variations among the different species

The three species had different root system architectures, which could be attributed to different root growth strategies (Fitter, 1987; Hodge et al. 2009). The trait comparison results showed that *C. alata* seedlings had more rapid taproot growth than the other two species. Its taproot length was up to 11.78 cm in the first week, much longer than that of *C. capsularis* (2.87 cm) and *D. reticulatum* (4.27 cm). More rapid root growth led to a larger root morphological size: *C. alata* had larger root surface area, length, and volume than the other two species. Interestingly, *D. reticulatum* had the highest biomass allocation to roots, but had the fewest lateral roots, and similar root volume and total length to *C. capsularis*. Previous studies have investigated root variations among different species and proposed some explanations (Comas and Eissenstat 2009; Liu et al. 2010; McCormack et al. 2012;
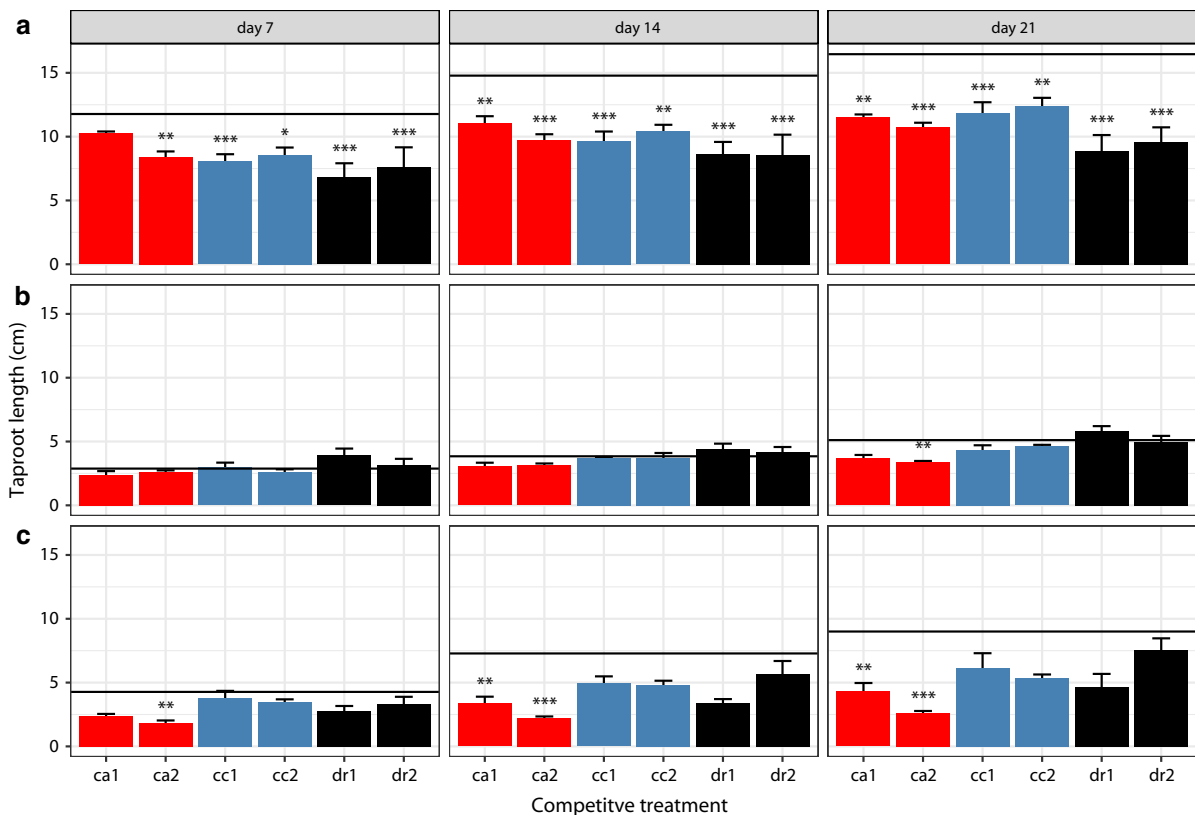
Fig. 4 The phytometer taproot length in the competition. **a** The phytometer is *C. alata*; **b** the phytometer is *C. capsularis*; **c** the phytometer is *D. reticulatum*. The x-coordinate represents the competitor identity and density. "ca", "cc", "dr" are the abbreviation of *C. alata*, *C. capsularis* and *D. reticulatum*, respectively. The number indicates the competitor density. For example, "ca1" refers to competing with one *C. alata* individual. The horizontal lines indicate the mean taproot length of the phytometer in single planting. The bar annotation * indicates the different levels between single planting and neighbour treatment, with * meaning $p < 0.05$, ** meaning $p < 0.01$, *** meaning $p < 0.001$, and no bar annotation meaning no significant difference

Kong et al. 2014). It was suggested that a root resource economic spectrum might exist (Mommer et al. 2012; Freschet et al. 2010; Reich 2014); that is, roots with higher specific root length and nitrogen:carbon ratio, and lower tissue density, would have higher nutrient acquisition ability and a shorter root lifespan (faster turnover). Therefore, it is highly possible that *C. alata* adopts a faster root economic strategy with fast root growth and high nutrient absorbing ability compared to the other two species. *D. reticulatum* roots are thicker and in closer contact than those of the other two species, adopting a conservative economic strategy. *C. capsularis* also has large specific root length, but its root system grows slowly compared to *C. alata*. Some other factors such as allocation strategy and resource use efficiency may also limit *C. capsularis* root growth (Weemstra et al. 2016). Multidimensional

trade-off possibly exists in plant root development. *C. capsularis* might allocate more resources to the production of secondary metabolites for defense and less to growth (Kramer-Walter et al. 2016). Low resource use efficiency could also possibly impede the root growth of *C. capsularis*. But the verification of these assumptions requires further study.

Competitive superiority of *C. alata*

Previous studies claimed that invasive plants might gain competitive superiority through fast growth, but whether rapid root growth might lead to competitive advantage (Gioria and Osborne 2014) or which part (shoot or root) played the key role was not tested. Although we didn't separate root and shoot competition in this study, the growth and trait differences

Fig. 5 The relationship between the total root length of competitors and traits of phytometers at day 21 after germination. The line annotation * indicates the significance levels of the relationships, with * meaning $p < 0.05$, ** meaning $p < 0.01$, and no annotation meaning no significant relationship. "ca", "cc", "dr" are the abbreviation of *C. alata*, *C. capsularis*, *D. reticulatum*, respectively. All the competitor total root length's degrees of freedom are 31
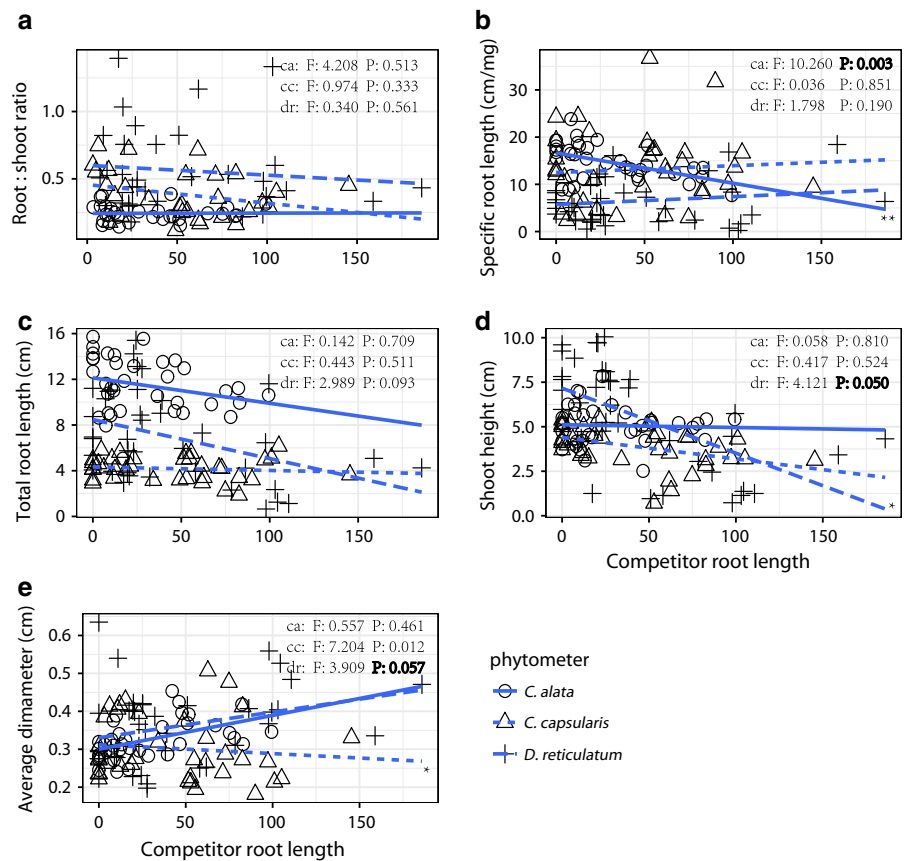
among the three species can help us infer the origin of the competitive advantages of invasive shrub *C. alata*. First, *C. alata* didn't exhibit any advantages in shoot height. *C. alata* seedlings had short shoot height compared to *D. reticulatum* at day 21 and similar shoot height with *C. capsularis* in all three periods (Fig. 1b). Shoot height is one of the most important factor in determining the light interception ability of plant (Kraft et al. 2015; Kunstler et al. 2016), thus it is unlikely that the competitive superiority of *C. alata* seedlings is caused by high light competitive ability. Although native shrub *D. reticulatum* shoot was higher than the other species at day 21, it didn't perform better in interspecific competitions (Fig. 3). Meanwhile, *C. alata* had much faster root growth in regarding to taproot length, total root length and root surface area. Previous studies have verified that these root traits were highly correlated with the root acquiring ability of nutrients and water (Chen et al. 2013; Valverde-Barrantes et al. 2017). Thus, the competitive superiority of *C. alata* may be mainly

due to its fast taproot growth and large root morphological size. On the contrary, naturalized, non-invasive *C. capsularis* had similar performances in competitions with native *D. reticulatum*, possibly due to their similar taproot growth and total root length. These results can also partly explain why *C. capsularis* cause no significant impact on local communities.

The fast seedling root growth might improve both response and effect abilities in competition (Goldberg 1990). Previous studies suggested that more competitive species might suffer more from intense intraspecific competition compared to less competitive species (Gersani et al. 2001), but we did not observe that. Although *C. alata* was very competitive, the seedlings of *C. alata* had less biomass reductions in intraspecific competition under high competitor density than those of the other two species (Fig. 4a). The fact that *C. alata* reduced its taproot growth (Fig. 4a) and specific root length in competitions (Fig. 5b) may be an active strategy to decrease competition. The long taproot and large root surface area of *C. alata* may also

improve its ability to explore outside the high competition zone, mitigate the damage from competition, and improve responsiveness (Wang et al. 2010; Craine and Dybzinski 2013; Trinder et al. 2013).

C. capsularis and *D. reticulatum* had dramatic biomass reduction when competing with *C. alata* (Fig. 3), reflecting the high competitive intensity. Some studies have noted that root competition is asymmetric when competition is for resources that are fast moving, such as nitrates and water (Schwinning and Weiner 1998; Craine et al. 2005; Funk and Wolf 2016). *C. alata* seedlings may preempt competition for those resources, limiting the growth of *C. capsularis* and *D. reticulatum*.

Density effect

It appears that increasing competitor density does not always increase the competition effects. When the root sizes of competitors and phytometers were relatively small such as for *D. reticulatum* and *C. capsularis*, increasing competitor density amplified the competition effects on phytometers (Fig. 4a, d). However, increasing *C. alata* density had less influence on competition effects (Fig. 4a–c). It is possible that the competitors saved some energy for intraspecific competition when density increased. There may exist a competitor density upper limit in root competition, limiting the infinite increase of competition effects on neighbors. Here, we only use two density levels. The density effects on root competition need more study in the future.

Root competition and shoot competition

Root competition has a complex relationship with shoot competition in the field (Belcher et al. 1995; Kiær et al. 2013). In different developmental stages or habitats, root and shoot roles in competition may change (Craine and Dybzinski 2013). For example, weak root competitiveness can inhibit shoot growth, which reduces the ability of plants to compete for light (Coomes and Grubb 2000). In this study, the shoot height of *C. capsularis* and *D. reticulatum* seedlings decreased as the competitor total root length increased (Fig. 5d). Therefore, the height advantage of *C. capsularis* and *D. reticulatum* may be diminished when competing with *C. alata*.

Despite this complexity, studies on community invasibility, disturbance history, and soil nutrient conditions may provide some insights into the relationship between root and shoot competition. Burke and Grime (1996) conducted a long-term field experiment and found that communities subject to disturbance and eutrophication were more invaded. Davis et al. (2000) proposed that communities with fluctuating resources were more susceptible to invasion. Root competition of seedlings may be critically important in these cases as disturbance reduces light competition and provides more chances for seeds to germinate simultaneously (Weiner 2004). For example, Rajaniemi et al. (2003) reported that, after fertilization, diversity decreased when root competition occurred, but there were no diversity changes when trenching was used to impede root competition. Therefore, root competition may predominate in invaded habitats, and the root competitive advantage of invasive plants may determine the community structure in these areas. We need more empirical study to test these hypotheses. Furthermore, the competition in this study is at the early seedling stage and we did not separate the shoot and root competition. Field experiments that separate the shoot and root competition and have longer growth duration might be further studied in the future.

Conclusion

Our study demonstrates that fast root growth may be an important factor in explaining the competitive advantages of invasive plants. In the future, more attention should be paid to root traits and belowground competition in the study of plant invasions. Many new techniques such as transparent growth system, minirhizotrons, isotope labeling, and X-ray computed tomography (Luo et al. 2004; Maeght et al. 2013; Klein et al. 2016) may provide more effective ways to study plant roots in situ. We may use these techniques to expand our research and observe the root growth of invasive plants in the field. At the same time, we know little about how root competition influences the population dynamics of invasive plants and the community structures of invaded habitats. The trenching method (Savage et al. 2013), an easy tool to separate root and shoot competition in the field, could be used to investigate the effects of root competition

on the population dynamics of invasive plants and community assembly.

Author contributions MN and SF conceived the project and designed the experiments. NM conducted the experiments and analyses. MN, YL, CC, HX and SF wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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