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Clonal growth strategies of *Reynoutria japonica* in response to light, shade, and mowing, and perspectives for management

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Abstract

Many of the most invasive plant species in the world can propagate clonally, suggesting clonality offers advantages that facilitate invasion. Gaining insights into the clonal growth dynamics of invasive plants should thus improve understanding of the mechanisms of their dominance, resilience and expansion. Belonging to the shortlist of the most problematic terrestrial invaders, *Reynoutria japonica* var. *japonica* Houtt. (Japanese knotweed) has colonized all five continents, likely facilitated by its impressive ability to propagate vegetatively. However, its clonal growth patterns are surprisingly understudied; we still do not know how individuals respond to key environmental conditions, including light availability and disturbance. To contribute to filling this knowledge gap, we designed a mesocosm experiment to observe the morphological variation in *R. japonica* growth in homogeneous or heterogeneous conditions of light stress (shade) and disturbance (mowing). Rhizome fragments were planted in the middle of large pots between two habitat patches that consisted of either one or a combination of the following three environmental conditions: full light without mowing, full light with frequent mowing, or shade without mowing. At the end of the experiment, biomass and traits related to clonal growth (spacer and rhizome lengths, number of rhizome branches, and number of ramets) were measured. After 14 months, all individuals had survived, even those frequently mowed or growing under heavy shade. We showed that *R. japonica* adopts a 'phalanx' growth form when growing in full light and a 'guerrilla' form when entirely shaded. The former is characteristic of a space-occupancy strategy while the latter is more associated with a foraging strategy. In heterogeneous conditions, we also showed that clones seemed to invest preferentially more in favorable habitat patches rather than in unfavorable ones (mowed or shaded), possibly exhibiting an escape strategy.

These observations could improve the management of this species, specifically by illustrating how aggressive early control measures must be, by highlighting the importance of repeated mowing of entire stands, as this plant appears to compensate readily to partial mowing, and by informing on its potential responses towards the restoration of a cover of competitive native plants.

Keywords

clonal growth, environmental heterogeneity, *Fallopia japonica* (*Polygonum cuspidatum*, Japanese knotweed), invasion dynamics, lateral expansion of patches/stands, spatial spread, vegetative regeneration

Introduction

Clonality is an attribute frequently associated with plant invasiveness (Lloret et al. 2005), and many of the most invasive plants in the world are clonal (Liu et al. 2016; Lowe et al. 2000; Pyšek and Richardson 2007). This is not surprising, as the highly plastic modular growth form of clonal plants releases them from many constraints related to being sessile. In clonal plants, resource-acquiring structures (leaves and root tips) are located on units called ramets (i.e. potentially autonomous physiological individuals; in other words, aerial shoots and their associated roots) that are projected into the environment by stolons or rhizomes, which serve as spacers between other resource-acquiring structures (Hutchings and de Kroon 1994). Although ramets are fixed in space, whole clonal fragments (i.e. physical individuals composed of all interconnected ramets) can spread laterally and may exhibit a large mobility (Oborny and Cain 1997; Zobel et al. 2010). By plastically changing the length, direction and/or number of spacers, clonal plants are able to exhibit complex behaviors such as precision foraging and selective ramet placement, escape strategies, or division of labor through ramet specialization (de Kroon and Hutchings 1995; Gao et al. 2012; Hutchings and Wijesinghe 1997; Oborny et al. 2012). These highly adaptable abilities can even potentially be transferred asexually through epigenetic trans-generational inheritance (Latzel and Klimešová 2010; Latzel et al. 2016). Clonality also enables survival and persistence of populations in absence of sexual reproduction (Eriksson 1997), rapid cover of and dominance of invaded sites (Herben and Hara 1997; Pyšek 1997) and, through clonal integration, the exchange of water, nutrients, carbon and information between connected ramets to reduce resource shortages and mitigate the effects of stress and disturbance (Jónsdóttir and Watson 1997; Liu et al. 2016). Out of these many advantages, some have been shown to be particularly associated with invasiveness such as high root foraging abilities or clonal integration (Keser et al. 2014; Song et al. 2013). Yet, many unknowns remain regarding the link between clonality and invasiveness, and the study of clonal invaders can help lay the foundation required to address fundamental and applied ecological questions (Liu et al. 2016; Yu et al. 2016).

At the local scale, since performance and impact of invasive clonal plants are often directly related to their clonal growth characteristics (e.g. architectural traits, lateral growth rate, ramet density, clonal integration, growth strategies), understanding clon-

al growth patterns and strategies is of prime importance for improving management strategies. This is why the clonal growth dynamics of many highly problematic clonal invaders have been the subject of extensive research over the years: e.g. *Phragmites australis* (Amsberry et al. 2000; Bellavance and Brisson 2010; Douhovnikoff and Hazleton 2014), *Carpobrotus edulis* (Roiloa et al. 2010; Roiloa et al. 2013), *Solidago* spp. (Hartnett and Bazzaz 1983; Jakobs et al. 2004; Stoll et al. 1998).

Despite being listed as one of the worst invasive plants in the world (Lowe et al. 2000), Japanese knotweed (*Reynoutria japonica* var. *japonica* Houttuyn) and its strong clonal growth abilities remain understudied. Capable of early and rapid growth by remobilizing resources stored in its rhizomes, *R. japonica* often forms dense monoclonal stands that exclude many native species and are also a nuisance for various human activities (Beerling et al. 1994; Lavoie 2017). Populations of *R. japonica* are extremely difficult to control (Child and Wade 2000; Delbart et al. 2012) and have, mainly by vegetative spread, successfully colonized most temperate regions of the world (Alberternst and Böhmer 2006; Beerling et al. 1994). In its native range, in the specific environment of Japan's high elevation volcanic deserts, several studies reported that clonal fragments of *R. japonica* var. *compacta* expand by reiterating a fixed pattern of sympodial rhizome growth (at the end of which clumped ramets are produced) with a high degree of clonal integration among ramets of different size to avoid asymmetric competition (Adachi et al. 1996a; b; Suzuki 1994). In its introduced range however, investigations on the clonality of *R. japonica* have mainly focused on its regeneration capacities (e.g. Bímová et al. 2003), or on resource translocation (Price et al. 2002). Two modelling studies also tried to understand the development of *R. japonica*'s clonal fragments by implementing growth rules derived from the Japanese studies. Yet, they recognized that their results were subject to serious restrictions due to the lack of quantitative data on the variability of clones' growth and demography in various environmental conditions (Dauer and Jongejans 2013; Smith et al. 2007). Consequently, we are still ignorant of how clonal fragments of *R. japonica* grow and expand in the wild and how they respond to environmental factors.

Two important features of environments that correspond to two main means of managing *R. japonica* are light availability and disturbance. *Reynoutria japonica* is mainly found in high-light habitats, but closed-canopy habitats such as forests can still be colonized either directly from vegetative propagules, or from the lateral expansion of surrounding populations (Beerling et al. 1994; Tiébré et al. 2008). Because closed-canopy habitats diminish the performance of *R. japonica*, restoration using competitive native species is increasingly used in control efforts (Dommanget et al. 2013). While many types of disturbance may facilitate invasion of *R. japonica* (Martin 2019; Pyšek and Hulme 2005), mowing is a disturbance that is used as the main control technique against *R. japonica* in many regions. Mowing is done either across entire stands or just on part of a stand, for example on roadsides or at the border between two properties (Delbart et al. 2012; Schifflleithner and Essl 2016). It is likely that the clonal dynamics of *R. japonica* vary substantially between the possible combinations of these environmental factors: i.e. whole connected clones or parts of

clones growing in full light or under a closed canopy, and being mowed or not. For instance, some authors report that shaded clones usually display a lower ramet density than the ones growing in open areas (Dommanget et al. 2019; Martin et al. 2019) or that, conversely, mowing increases ramet density and favors stands' expansion (Beerling 1990; Child and Wade 2000).

To improve our understanding of *R. japonica*'s invasion dynamics, specifically how clonal growth responds to important environmental factors, we designed a mesocosm experiment. In it, we explore how the development and expansion of young clonal fragments is affected by homogeneous or heterogeneous conditions of light stress (shade) and disturbance (mowing). We aimed to better understand plant growth strategies and potential trade-offs when faced with more or less favorable habitats, and investigate how these responses might be relevant to improved management of *R. japonica* by mowing/cutting or by ecological restoration using dense cover of competitive species. We hypothesized that: i) a homogeneously high light availability would favor aggregation of ramets while a homogeneous shade would favor a more scattered distribution of aerial shoots, two growth forms respectively known as phalanx and guerrilla (sensu Lovett Doust 1981); ii) mowing would release axillary buds from apical dominance, therefore favoring higher rhizome branching frequency and ramet density than in un-disturbed *phalanx* clones; and iii) individuals that are partially stressed (shaded) or disturbed (mowed) would try to 'escape' these less favorable habitats by investing more in the growth of their parts growing in high light and undisturbed areas.

Materials and methods

Biological material

In April 2017, rhizomes belonging to a single *R. japonica* individual were manually excavated. The plant was located outside the village of Cholonge (1061 m a.s.l.; 45°00'N–5°79'E), in the French Alps. This individual was chosen because it was growing in an open and unmanaged site. This was an important prerequisite since we wanted to limit the chance that ramets growing from its rhizome fragments were influenced by stressful or disturbed conditions via transgenerational inheritance (Latzel and Klimešová 2010; Latzel et al. 2016). Recent evidence showed that a single *R. japonica* genotype can exhibit differing phenotypes determined by the growing conditions of their "parental" populations, due to epigenetic variation (Zhang et al. 2017).

Following excavation, rhizomes were washed and cut to obtain homogenized fragments with the same approximate weight and number of nodes. The thirty most similar fragments were selected, bagged and stored in a cold room before the start of the experiment. These fragments had a mean weight of 16.44 g (\pm 0.85 g) and a mean number of nodes of 8.06 (\pm 2.46).

Experimental design

The mesocosm experiment was conducted in an experimental nursery of the National Forest Office (ONF) located in Guéméné-Penfao, Brittany (France). The area is characterized by mean monthly temperatures ranging from 7.9 to 16.4°C, and 694 mm of mean annual precipitation (data from Rennes meteorological station; www.meteofrance.com).

The experimental design was composed of five treatments with six replicates each. The treatments were designed to enable us to evaluate how *R. japonica* responds to homogeneous or heterogeneous environmental stressors. Each plant was grown in pots divided into two habitat patches. These habitat patches were identical for homogeneous treatments: light without mowing (L), light with mowing (M), and shade without mowing (S). For heterogeneous treatments, they differed: half-light – half-mowing (LM) and half-light – half-shade (LS); Fig. 1).

Large pots for this experiment were created from thirty rainwater tanks of ca. 1000L (120 × 100 × 116 cm) by cutting off their tops. Pots were first filled with a 15 cm layer of gravels (Ø 0–32 mm) to facilitate water drainage through an outlet pipe. On top of

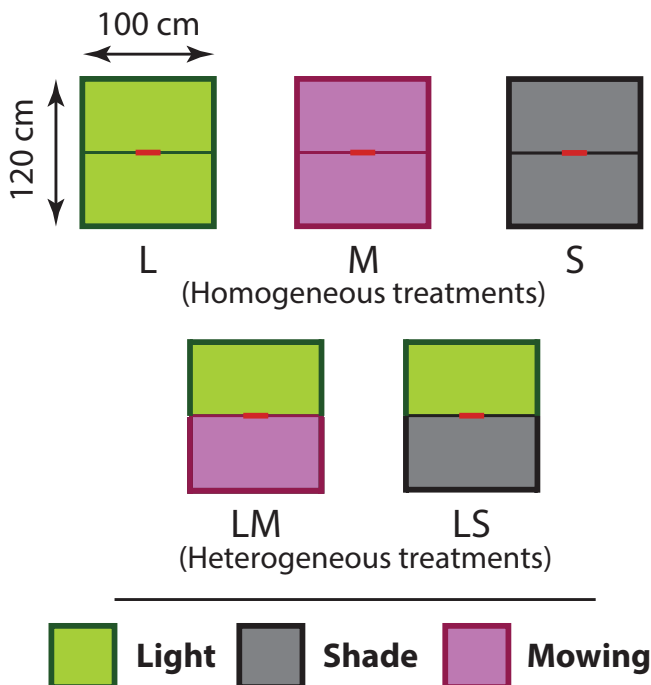


Figure 1. Experimental design. The different colors represent the treatments: green (un-shaded and un-mowed habitat), pink (un-shaded but mowed habitat) and grey (shaded but un-mowed habitat). Each of these five different treatments had six replicates. The red segments in the middle of “pots” represent the position of the rhizome fragments that were planted

that, we added approximately 100 cm layer of a certified substrate composed of 70% river sand, 15% loam and 15% compost (chemical composition of the substrate: N = 1.2%; K₂O = 1.4%; P₂O₅ = 0.4%; MgO = 0.6%; CaO = 2.1%; C:N = 12; pH = 8–9). Shade treatments (S and LS) were created by inserting 3 m poles into the pots and covering them with netting that filtered around 80% of the light. Pots were arranged in a flat area, with their location and orientation randomly chosen in such a way that each replicate of a given treatment had a different orientation from the other five replicates. To avoid the effect of projected shadows caused by the tall shade treatments, pots were separated by 4 m intervals in every direction. Additionally, the randomized placement and orientation of all the pots was reshuffled in the middle of the experiment.

In early May 2017, the thirty rhizome fragments were randomly assigned to one of the pots. They were buried two centimeters below the surface in the middle of the pots, orthogonally to the greater length of the pots. This position coincided with the limit between the two habitat patches of the pots (Fig. 1). In mowed habitats (M and LM), the aerial shoots of ramets were manually clipped and removed every time they reached approximately 25 cm in height. This resulted in three mowing events during the first vegetative season, and one during the following spring two weeks before the end of the experiment. This mowing frequency was chosen because it reflects regular management along many French roads and railways. Throughout the experiment, pots were weeded regularly and water availability was maintained using a multi-point dripping irrigation system. We also checked for potential differences in air temperature and soil humidity using ten TMS-4 data-loggers (www.tomst.com) randomly placed in treatments' modalities, left two weeks, and moved to another random replicate of the same modality.

Harvest and measurements

Before each mowing event, the number of ramets in each habitat patch was recorded. We decided to stop the experiment when ramets began to reach pots' edges, to minimize obstacle-effects on the clonal architecture of the plants (duration of the experiment = 420 days; ca. 14 months).

The experiment was harvested at the end of June 2018. All ramets growing above-ground in all habitat patches were counted before being clipped and oven-dried for 48h at 100 °C prior to measuring dry biomass. Additionally, the horizontal distance between the farthest ramet and the center of the pot (i.e. the location of the rhizome fragment initially planted) was measured for each half of each pot to estimate maximal lateral expansion distances for developing stands. We then carefully excavated the plants, using mostly our hands and screwdrivers in order not to break fragile rhizomes and buds, and to extract rhizomatous systems as intact as possible. However, roots were intentionally cut to facilitate excavation, as our hypotheses were unrelated to the root system. We then marked the position of the separation line between the two habitat patches on each rhizomatous system before removing the dirt with an air compressor and brushes. Rhizome and spacer lengths (see below), number of rhizome branches,

and number of axillary and basal buds that were growing in each habitat patch were measured. Finally, we also measured rhizome biomass with the same method as for aboveground tissue.

We follow Sachs' (2002) definition of "spacers" as plagiotropic stems, in this case rhizomes, whose apices produce new ramets. Rhizomes, however, do not always produce ramets as they may be dormant, broken, dying, or still growing. Consequently, all *R. japonica* spacers are rhizomes (with new ramets at their end), but not all rhizomes are spacers. In this study, spacer length corresponds to the distance between the location on the mother rhizome whence the spacer branched and the first aboveground node of the nascent ramet's aerial shoot.

Statistical analyses

Prior to analyses, data were explored and prepared following the protocol of Zuur et al. (2010). When required, data were log transformed to ensure homoscedasticity among groups.

Since *R. japonica*'s clonal growth patterns and processes are largely unknown, the first steps of our analyses were necessarily exploratory and descriptive. To investigate our hypotheses however, the responses of variables characterizing *R. japonica*'s growth form and strategies were analyzed more thoroughly. These variables were biomass (aboveground, rhizomatous and total dry biomasses in grams), specific spacer length (length of a spacer per unit of biomass), number of ramets (accounted for as the number of aerial shoots) and rhizomes' branching frequency (calculated as the number of rhizome branches per unit of rhizome length). Analyses were performed at two different scales: (i) pots and (ii) half-pots. As a reminder, in our experimental design there were two habitat patches per pot, identical or not, but only one plant (Fig. 1), that is, one *R. japonica* individual/clonal fragment. Consequently:

- (i) At the *pot scale*, measurements made within the two habitat patches of each pot were summed up so as to have observations at the individual level. As such, whole plants were taken as statistical units and our five treatments (L, M, S, LM, and LS) were used as explanatory factors. For each response variable, we performed ANCOVAs with type II Sums of Squares and used the weight and number of nodes of initially planted rhizomes as covariates. For multiple comparisons, we used pairwise *t*-tests using Holm-Bonferroni corrections to control for family-wise error rates.
- (ii) At the *half-pot scale*, observations were made at the sub-individual level (i.e. half plants) and differences linked to differing growing conditions between habitat patches were investigated, but only for replicates belonging to heterogeneous treatments (LM and LS). As the two half-plants of each pot were not independent, we used mixed-ANCOVAs with *pot* as a random effect (Rutherford 2011). Post-hoc tests were performed using Tukey's HSD test to account for possible violations of sphericity.

Initially, we also wanted to study potential differences in the number of buds between treatments as evidence of habitat selection, but we observed during harvest that *R. japonica* produces a bud at each node regardless of the treatment, precluding further analysis.

All analyses were performed with R version 3.5.2 (R Development Core Team 2019).

Results

General observations and biomass production

Consistent with what is reported in the literature (Adachi et al. 1996a; Bailey et al. 2009), clonal fragments expanded through the repeated sympodial branching and growth of rhizomes. One or several rhizomes emerged from the lateral buds or node meristems of the initially planted rhizomes. These new rhizomes quickly curved upward to produce ramets, and then new lateral rhizomes sprouted and grew farther off in a concave fashion to produce new ramets and so on. Unfortunately, the precise timing of rhizome branching could not be investigated with our experimental setting nor could the factors inducing branching or the upward bending of rhizomes. In all treatments, mortality of individual ramets (not whole clones) was observed during the first growing season, even in undisturbed pots, and this mortality did not seem to be related to overcrowding and intra-plant competition. Conversely, some habitat patches harbored no ramets for months until their number quickly increased after a first ramet colonization.

All rhizomes that were planted at the beginning of the experiment gave birth to clonal fragments that survived throughout the 14 months of the experimentation. Interestingly, most clones produced flowers in the first growing season except those of the entirely mowed treatment (M).

As expected, most traits related to clonal growth varied strongly by treatment (Tables 1, 2; Figs 2–5). In little more than a year, the largest clones produced over 1.9 kg of dry biomass (without roots) and over 21 m of rhizomes, with some spacers reaching 112 cm (Table 1).

Clones in the L treatment (full light without mowing) produced their farthest ramets (from their center) farther than individuals of any other treatments and with a far lower variability (Table 2). As such, after 14 months, clones growing in full light without mowing possessed a mean radius exceeding 56 cm while entirely mowed (M) or shaded (S) clones displayed mean radiuses of around 12 and 34 cm, respectively (Table 2).

In all our analyses, covariates did not significantly influence examined responses. Consequently, observed differences could be attributed to treatments. Unsurprisingly, shade and mowing treatments significantly reduced total biomass production ($F = 89.36$; $\text{dfn} = 4$, $\text{dfd} = 26$; $p < 0.001$), aboveground biomass production ($F = 43.18$; $\text{dfn} = 4$, $\text{dfd} = 26$; $p < 0.001$) and rhizomatous biomass production ($F = 57.03$; $\text{dfn} = 4$, $\text{dfd} = 26$; $p < 0.001$; Fig. 2a). With the exception of the pairs L-LM ($t = 1.532$, $p = 0.145$) and LM-LS ($t = 1.383$, $p = 0.096$), all differences in mean total biomass were significant. For homogeneous treatments, the hierarchy of differences remained the same for

Table 1. Summary statistics of descriptive variables measured across all treatments (at the pot scale).

	Maximum spacer length (cm)	Mean spacer length (cm)	Cumulated rhizome length (cm)	Mean rhizome length (cm)	Longest length between opposite ramets (cm)	Number of rhizome branches	Number of buds (on rhizomes)	Number of ramets (aerial shoots)	Aboveground dry biomass (g)	Rhizomatous dry biomass (g)	Total dry biomass (g)
Mean	56,07	30,59	599,2	16,65	68,98	24,6	230,42	23,97	499,45	207,04	706,49
Standard deviation	29,22	24,55	519,03	6,94	39,43	24,4	159,3	13,25	404,48	200,8	591,5
Median	53,25	23,27	484,7	16,32	68	17,5	220,5	22,5	325,5	98,38	394,52
Minimum	17,1	1	38,9	3,367	6,5	1	19	5	1,21	9,01	10,22
Maximum	112	92,5	2113	29,18	133	97	638,92	55	1221	708,66	1902,66

Table 2. Descriptive statistics by treatment for the distance to the farthest ramet in each habitat patch (pot-half).

	L	M	S	LM	LS
Mean	56,17	11,63	34,50	53,83	36,58
Standard deviation	6,70	7,06	23,85	19,31	23,46
Median	56	11,5	38	57,5	34
Minimum	45	1,5	5	15	5
Maximum	66	25	70	75	66

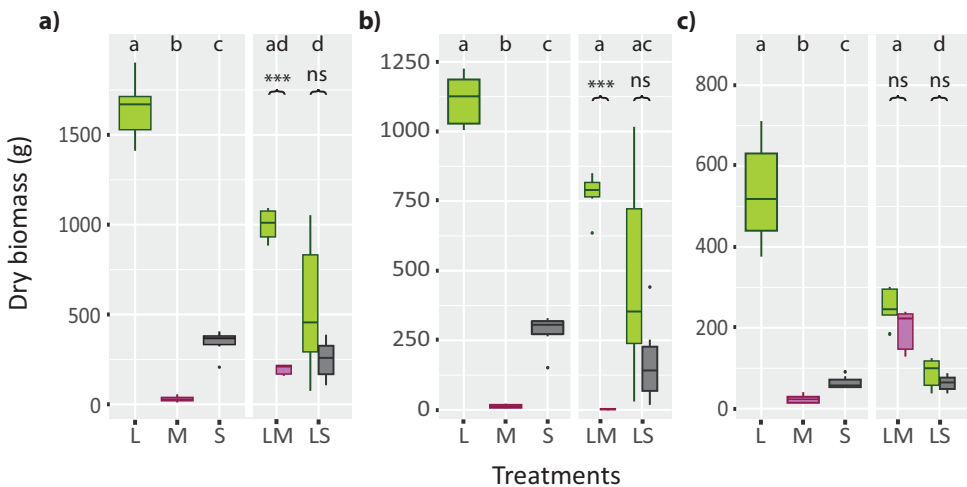


Figure 2. Differences in total dry biomass (a), aboveground biomass (b) and rhizomatous biomass (c) between the L (light), M (mowed), S (shaded), LM (half-light – half-mowed) and LS (half-light – half-shaded) treatments. For analyses at the pot scale, letters are used to indicate the significance level of differences (treatments not sharing the same letter were significantly different at $p < 0.05$). For analyses at the half-pot scale, stars are used to indicate significant differences between habitat patches (* = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$; ns = not significant). As a reminder, differences among pot-halves have only been investigated for heterogeneous treatments (i.e. LM and LS).

aboveground and rhizomatous biomasses. On the other hand, although clones growing in the LM treatment did not differ significantly from the LS treatment with respect to aboveground biomass ($t = -1.523, p = 0.555$), they produced significantly more rhizomatous biomass ($t = -3.844, p = 0.007$; Fig. 2b, c). Among heterogeneous treatments, at the half-pot scale, plant parts growing in the favorable habitat patches (i.e. un-mowed and undisturbed) of the LM treatment presented a significantly higher aboveground ($t = 14.609, p < 0.001$) and total biomass ($t = 12.72, p < 0.001$) than parts growing in the mowed halves of these pots (Fig. 2a, b). No significant differences in any type of biomass production were found among habitat patches of the LS treatment, nor in rhizomatous biomass production between pot-halves of the LM treatment (Fig. 2a–c).

Spatial exploration and clonal traits

At the scale of pots, individuals of *R. japonica* growing in full light without mowing (L) had significantly lower specific spacer lengths than clones growing in fully shaded habitats (S; $t = 4.361, p < 0.001$) and entirely mowed individuals (M; $t = 3.005, p < 0.025$). At the half-pot scale, despite a slight trend of increased specific spacer length for spacers growing in the shaded habitat patches of the LS treatment, no significant differences were found within or among heterogeneous treatments (Fig. 3).

Shading (S) led to the production of fewer ramets than full light (L) ($t = -7.327, p < 0.001$) and mowing (M) ($t = -8.23, p < 0.001$), and there was no differences

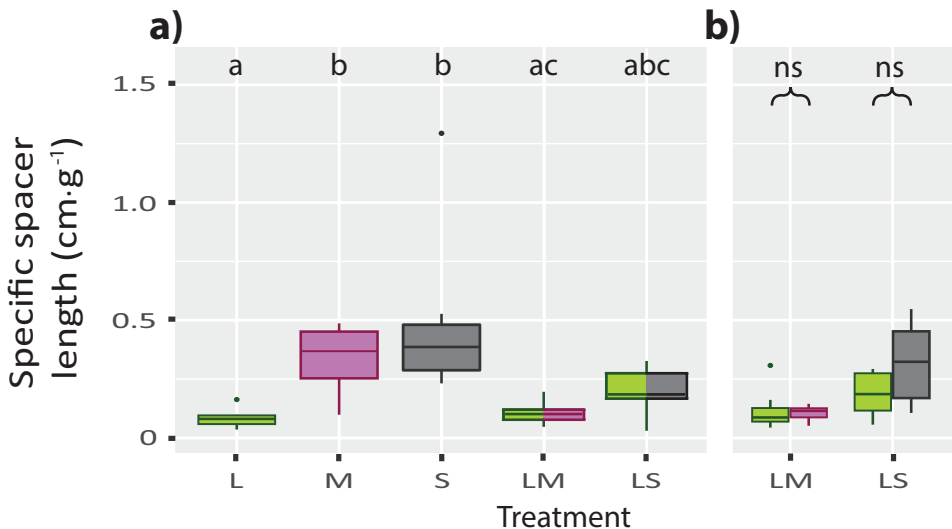


Figure 3. Differences in specific spacer length between L (light), M (mowed), S (shaded), LM (half-light – half-mowed) and LS (half-light – half-shaded) treatments at the scale of pots (a) or half-pots/habitat patches (b). Treatments not sharing the same letter are significantly different at $p < 0.05$, ns = not significant.

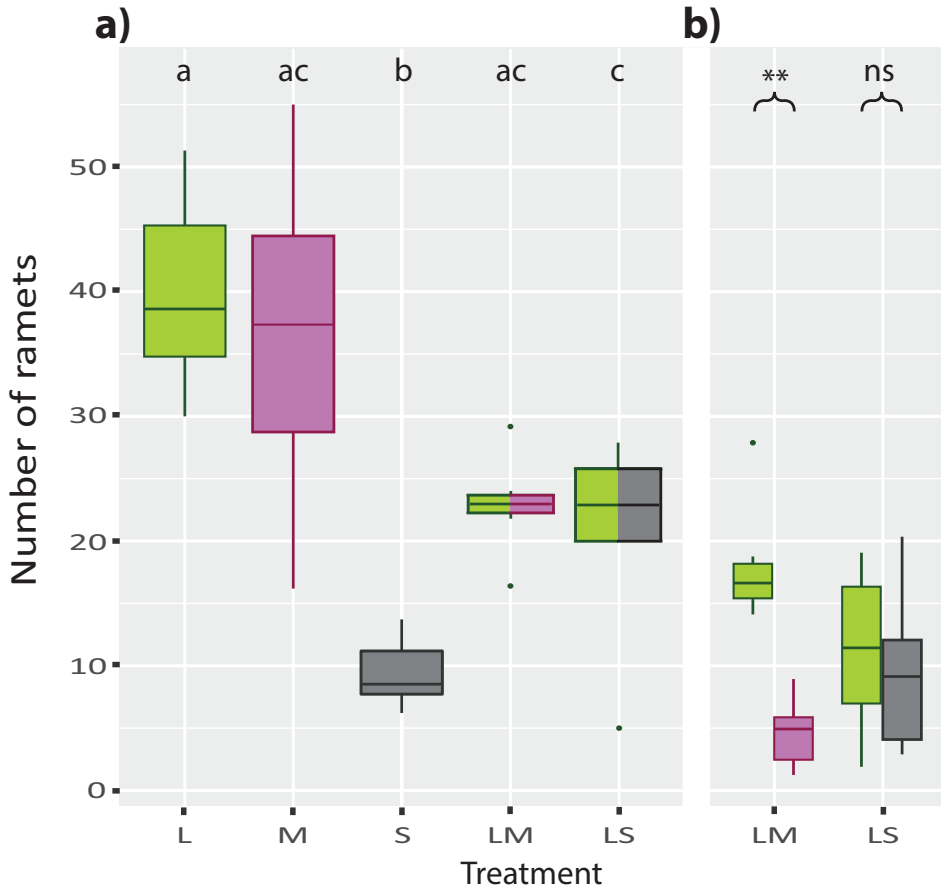


Figure 4. Differences in number of ramets between L (light), M (mowed), S (shaded), LM (half-light – half-mowed) and LS (half-light – half-shaded) treatments at the scale of pots (**a**) or half-pots/habitat patches (**b**). For the former, treatments not sharing the same letter were significantly different at $p < 0.05$, while for the latter: * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$; ns = not significant.

between full light and mowing in number of ramets ($t = 0.276$, $p = 0.89$; Fig. 4a). Interestingly, at the half-pot scale, the un-mowed habitat patches of the LM treatment displayed significantly more ramets than mowed habitat patches ($t = 5.73$, $p = 0.002$). Such pattern among the two habitat patches of LM treatment's individuals is therefore not consistent with the pattern observed in their homogeneous treatment counterparts (namely clones in L and M treatments) that possessed similar number of ramets (Fig. 4a, b).

Finally, clones in pots receiving full light (L) had a significantly higher rhizome branching frequency than shaded clones (S) ($t = -2.686$, $p = 0.032$), but not higher than entirely mowed clones (M; $t = 0.393$, $p = 0.267$) while LM and LS clones showed intermediate values (Fig. 5a). At the half-pot scale, once again, no significant differenc-

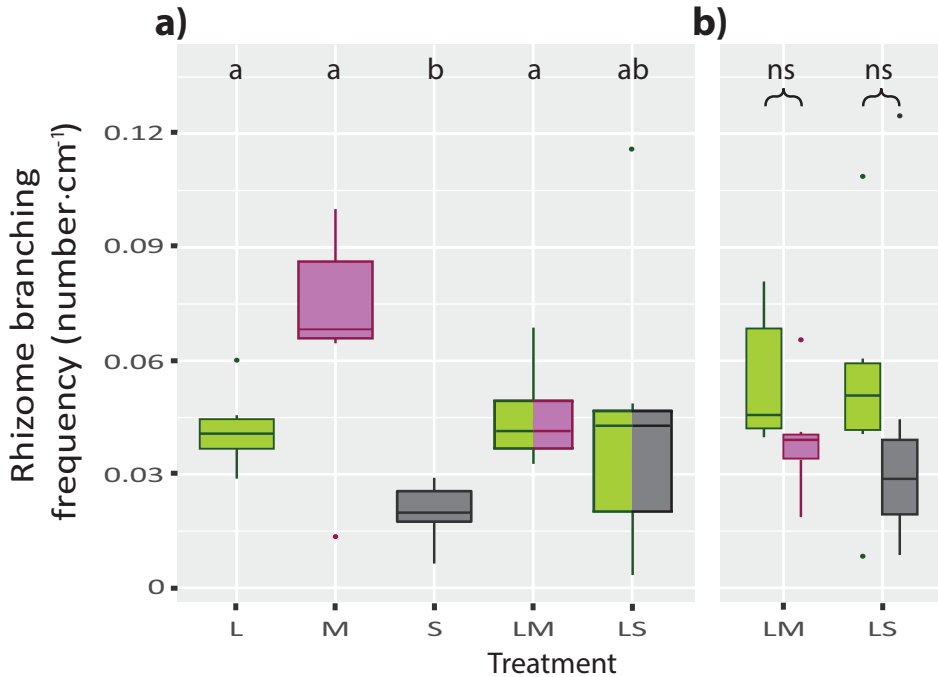


Figure 5. Differences in rhizome branching frequency (measured as the number of branches per unit of rhizome length) between L (light), M (mowed), S (shaded), LM (half-light – half-mowed) and LS (half-light – half-shaded) treatments at the scale of pots (a) or half-pots/habitat patches (b). For the former, treatments not sharing the same letter were significantly different at $p < 0.05$, while for the latter: ns = not significant.

es in branching frequency were found between plant parts growing in habitat patches of the heterogeneous treatments LM and LS (Fig. 5b). Interestingly, rhizomes in unmowed halves of LM treatments had a seemingly higher branching frequency than rhizomes in mowed ones, therefore exhibiting a reverse pattern compared to individuals growing in homogeneous treatments L and M.

Discussion

Despite its importance for understanding and managing local invasion dynamics of *R. japonica* and its congeners, the clonal growth of this taxon and its variations under various environmental conditions have been surprisingly understudied (Bashtanova et al. 2009; Smith et al. 2007). The observations and data presented here represent, to the best of our knowledge, the first quantitative assessment of the clonal growth dynamics of *R. japonica* in various homogeneous or heterogeneous habitats.

Clonal growth forms and strategies

Our results show that *R. japonica* can respond plastically to the quality of its habitat in various vegetative growth traits. In accordance with our first hypothesis, *R. japonica* adopted a phalanx growth form when growing in a homogeneously illuminated habitat by aggregating many ramets separated by short spacers. Conversely, when growing under heavy shade, clones only presented a few ramets separated by long spacers, typical of a guerrilla growth form (Figs 3a, 4a). As these two growth forms were associated with different specific spacer lengths and rhizome branching frequencies (Figs 3a, 5a), they likely stemmed from differing clonal growth strategies and not only from differences in the vigor of clones.

Although clones growing in full light without mowing expanded laterally more than shaded ones in absolute values (Tables 1, 2), proportionally to their accumulated biomass (and thus for an equivalent vigor), the latter went further and explored more horizontal space than the former (Fig. 3a). It is therefore possible that, in shaded environments such as a forest understory, *R. japonica* displays an extensive foraging strategy to increase the chances of placing ramets in sunflecks and canopy gaps or to escape this less favorable habitat (cf. Lovett Doust 1981; Slade and Hutchings 1987a), as has been frequently reported for other species (de Kroon and Hutchings 1995; Slade and Hutchings 1987b; Xie et al. 2014). On the other hand, in a homogeneously luminous and undisturbed environment, *R. japonica* seems to adopt a space-consolidation strategy (sensu de Kroon and Schieving 1990). In this exploitative strategy, phalanx clones multiply their ramets through increased branching frequency and short spacer lengths in order to monopolize resources and limit interspecific contacts (de Kroon and Schieving 1990; Gough et al. 2001; Herben and Hara 1997; Lovett Doust 1981).

In theory, phalanx individuals should have a slower lateral expansion rate than guerrilla individuals (Lovett Doust 1981; Schmid 1986). Yet, Figure 2c and Tables 1, 2 show that *R. japonica* grew faster and explored more soil volume in 14 months when cultivated in full light than in a shady place, as long as it is undisturbed. This is consistent with observations made on cultivated *R. japonica*'s stands (i.e. composed of several competing clonal fragments) that expanded faster and further in two seasons when grown alone than when planted in mixture with a high density of *Salix viminalis* cuttings (Dommanget et al. 2019). In both cases, this difference is certainly explained by the higher vigor of clones growing in full light compared to shaded ones. Still, theory does not tell if the differences in lateral growth rates between phalanx and guerrilla individuals should be constant over time or not. It could be that, in order to operate an efficient spatial pre-emption against potential competitors, phalanx clones of *R. japonica* have a quick initial expansion rate for a while followed by a (gradual or steep) deceleration as clones get stronger and more dominant and as their chances of being excluded decline. In the long term however, guerrilla clones could perhaps expand further (to escape) or display a higher clonal mobility than phalanx ones (cf. Zobel et al. 2010). More long-term empirical studies are needed to verify these assumptions and

more generally, to assess the differences in lateral growth rates between clonal fragments of *R. japonica* growing in differing environments as no data actually exist on the matter.

Against our expectations, average ramet densities and branching frequencies of entirely mowed clones in full light (M treatment) were not significantly higher than those of illuminated but un-mowed ones (L treatment), despite interesting trends. Moreover, entirely mowed individuals had an overall very low spatial expansion. This discrepancy between our hypothesis and observations is likely due to the intensity of mowing events. As these clones had to cope three times with the total destruction of their aerial organs during their first growing season (and one more time at the beginning of the next one), their biomass production and spatial exploration must have been strongly constrained (Fig. 2; Table 2), hence limiting our ability to properly observe their clonal growth patterns in less disturbed environments. The intellectually appealing hypothesis stipulating that mowing breaks the apical dominance of *R. japonica*'s ramets and thus favors rhizome branching and the lateral expansion of clonal fragments (cf. Bashtanova et al. 2009; Beerling 1990) consequently requires further study.

Stands of *R. japonica* frequently grow in habitats that do not experience full sun, or are mowed, such as roadsides, semi-natural riverbanks or forest edges (Beerling et al. 1994; Martin et al. 2019; Tiébré et al. 2008). In those, we may expect clones to adopt tactics to cope with or to avoid the effect of less favorable areas. Unfortunately, at the half-pot scale, our clones grown in heterogeneous conditions did not demonstrate many significant differences between favorable (full light and undisturbed) and unfavorable (shaded or mowed) habitat patches for most studied traits. Yet, despite this overall lack of statistical significance, clone parts growing in the favorable habitat patches of our heterogeneous treatments appeared to have produced more rhizome branches (per unit of rhizome length), more ramets, and to have accumulated more rhizomatous biomass than parts growing in unfavorable patches (Figs 2c, 4b, 5b). These observations suggest that resources are preferentially invested locally and that the un-disturbed and un-shaded parts of clonal fragments do not support much the development of parts growing in less favorable conditions, possibly demonstrating early stages of habitat selection. Evidence from previous studies already suggested that in homogeneous conditions, the level of clonal integration between ramets of *R. japonica* varied with the level of resources (Price et al. 2002; Suzuki 1994). Our results show that environmental heterogeneity may also affect patterns of resource sharing in this taxon. Additionally, shaded patches of the LS treatment harbored parts of clones that seemed to exhibit higher specific spacer lengths (Fig. 3b), which could be evidence of a trade-off between phalanx and guerrilla growth forms (e.g. Ye et al. 2006) and thus, of a localized escape strategy.

The absence of clearer morphological and architectural responses in the heterogeneous treatments may be simply linked to the methodological constraints related to the cultivation of giant herbaceous species such as *R. japonica*: i.e. small sample size and short duration of experimentation. A longer experiment, with a harvest at the end of the second growing season could perhaps have given different results, for instance for the significance of observed differences or bud bank's distribution (cf. Gao et al. 2012; Ott and Hartnett 2015; Watson et al. 1997). Further research on this topic would be

useful to draw more definitive conclusions. Of course, we cannot rule out the possibility that *R. japonica* is purely unable to select a preferential habitat and that it does not attempt to escape through directional growth (e.g. Evans and Cain 1995; Sampaio et al. 2004) or selective placement of ramets (e.g. de Kroon and Hutchings 1995; Wijesinghe and Hutchings 1997).

In addition to increased sample size, it would be interesting if future experiments could increase the number of sampled populations. *Reynoutria japonica* is indeed known to be represented by the same single clone throughout most of its introduced range (Bailey et al. 2009). As such, sampling a single location was satisfactory to account for its genotypic variability, but not for potential epigenetic variations. Sampling populations along various environmental gradients could therefore potentially reveal different growth patterns (e.g. Richards et al. 2012; Zhang et al. 2017) that could help refining and expanding observations made in the present paper.

Establishment potential and management implications

Although this experiment did not aim at investigating the establishment potential of *R. japonica*, it is enlightening to observe that the thirty regenerating plants survived their first winter and were still growing after 14 months. It is even more interesting when we consider that some had to grow under heavy shade or in a frequently mowed environment. It confirms that three mowing events per year is not sufficient to kill regenerating clones of *R. japonica* (Seiger and Merchant 1997), though that may depend on the size of the propagule from which a plant is regenerating.

The vegetative propagules that we planted had a fresh weight of approximately 16 g, which represents rhizomes with a length of 12–13 cm for a diameter of 1.2 cm. Such dimensions are certainly not infrequent in the wild where *R. japonica* can annually produce underground biomass exceeding $10 \text{ t} \cdot \text{ha}^{-1}$ (Callaghan et al. 1981; Palmer 1994). Even our young clones produced enough biomass to recreate dozens of such propagules (Fig. 2c). At least two recommendations for the management of *R. japonica* can be made from these observations. Firstly, monitoring campaigns should not overlook shaded habitats as clones born from vegetative propagules may have established there. Secondly, early control campaigns should either favor the manual extraction of the whole regenerating ramets (e.g. Barthod and Boyer 2019), or remove or spray above-ground plant parts at a high frequency, to have a chance at eradicating newly established *R. japonica*.

Interestingly, clones that experienced only partial mowing (LM treatment) did not produce a significantly lower total biomass than un-mowed individuals (L treatment). Yet, the contrast with the biomass production of entirely mowed clones (M treatment) is striking (Fig. 2). It thus appears that clone parts growing in un-mowed halves of the LM treatment managed to compensate for the loss of their mowed counterparts. This is important from a management perspective as it emphasizes the need to mow/cut *R. japonica* individuals over their whole cover to truly impact their growth dynamics.

This observation gives a quantitative explanation to empirical and modelling studies indicating that low mowing frequency and/or partial mowing have close to no effects on the cover or expansion dynamics of *R. japonica* (Gerber et al. 2010; Lavallée et al. 2019; Martin et al. 2019).

Restoration of competitive native species has been shown to be a promising management solution to limit the performances and spread of *R. japonica* (Dommanget et al. 2015; Dommanget et al. 2019; Skinner et al. 2012). Control by restoration is notably interesting as it is thought to have low environmental impacts and pecuniary cost in the long-term (Dommanget et al. 2019). This kind of restoration using mostly plantings of local species to shade *R. japonica* is frequently associated with mowing during the first years of installation. In this context, it would therefore be very interesting to test the combined effect of shade and mowing on the long-term spatial dynamics of both regenerating and established clones. Besides, it would also be relevant to study the effect of other aspects of competition (not only for light) on the spatial exploration of knotweed clones. Long term studies will additionally be required to observe if *R. japonica* would be able to escape the cover of the planted native species through directional growth or spatial exploration.

Conclusion

To the best of our knowledge, this is the first time that quantitative observations of clonal growth and expansion dynamics in *R. japonica* are provided for differing environmental conditions. We believe that our results help improve our understanding of the invasion dynamics of this species at the local scale, highlighting aspects of its resilience and effects on invaded communities that will be useful for the management and modelling of this taxon. However, more research is needed to complete our results and to extend them to other knotweed taxa as well as to other epigenotypes of *R. japonica*.

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