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Research article

Ecological restoration combining mowing and competition limits the development of invasive *Reynoutria japonica*

Alice Michelot-Antalik [a,*], Alan Kergunteuil [a,b], Léa Genty [a,c], Paul Montagne [d], Christophe Robin [a], Mitra Tehranchi [e], Sylvain Lerch [f]

[a] *Université de Lorraine, INRAE, LAE, F-54000, Nancy, France*
[b] *INRAE, PSH, F-84000, Avignon, France*
[c] *Anses, Laboratoire de la Santé des Végétaux, 755 Avenue du Campus Agropolis, CS30016, F-34988, Montferrier-sur-Lez cedex, France*
[d] *SPIGEst ENSAIA, 2 Avenue de la Forêt de Haye BP 20163 54505 NANCY, France*
[e] *NOREMAT S.A., F-54710, Ludres, France*
[f] *Ruminant Nutrition and Emissions, Agroscope, 1725, Posieux, Switzerland*

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ABSTRACT

Limiting the negative effects of an invasive species, such as *Reynoutria japonica*, has become a challenge for scientists and a necessity for managers. Ecologically relevant, technically feasible, and sustainable control methods must be created to reduce the development or spread of *R. japonica* in ecosystems. The objective of our study was to investigate how monthly mowing in association with plant competition affects the development of *R. japonica* over a three-year field experiment. Among the plant traits measured, the height growth of *R. japonica* was the most affected; it was strongly reduced in the presence of competing plants. Combined mowing and competition with restoration plants negatively affected the growth diameter of *R. japonica*. Most competitive sown species were well established and complementary in limiting the development of *R. japonica*. The plant communities showed interannual dynamics in which *R. japonica* declined progressively. The restoration methodology adopted in this study allows managers to make appropriate decisions to reduce the impact of *R. japonica* on ecosystems.

1. Introduction

Invasive alien species have recently been ranked as the fifth direct anthropogenic driver of change in the global state of nature, with an overall impact of 11% (IPBES, 2019). Their number has been steadily increasing, particularly over the last few decades, with 37% of all initial species recorded over the past 200 years occurring between 1970 and 2014 (Seebens et al., 2017). Invasive plant species can affect socioeconomic activities (Bacher et al., 2018), ecosystem structures (Bartz and Kowarik, 2019; Pyšek et al., 2012; Ricciardi et al., 2013; Vilà et al., 2011), and ecosystem services (Vilà and Hulme, 2017) across all biomes (Weidlich et al., 2020). These impacts require improved management on regional, national, and global scales (Kettenring and Adams, 2011; Martin et al., 2020b).

Among the invasive species, *Reynoutria japonica* (Japanese knotweed, syn. *Fallopia japonica*, Polygonaceae) is considered by the International Union for Conservation of Nature (IUCN) as one of the 100 worst existing invasive species (Lowe et al., 2000), and it is one of the most concerning invasive species in northwestern Europe (e.g., Djeddour and Shaw, 2010). *R. japonica* originated in East Asia and was intentionally introduced in 1840 for ornamental, melliferous, and fodder purposes in the Netherlands (Bailey and Conolly, 2000). Populations of *R. japonica* have expanded exponentially since 1950 in Europe and cover many ecosystems, both terrestrial (e.g., fallow lands, forest margins, edges of transport infrastructures) and aquatic (e.g., riverbanks; Mandák et al., 2004). Such an invasion significantly reduces both species richness and the abundance of plants, gastropods, vertebrates (Hajzlerová and Reif, 2014; Maerz et al., 2005; Stoll et al., 2012), and soil bacteria (Lavoie, 2017). In addition to ecological disorders, *R. japonica* causes damage to transport infrastructures and riverbank collapses, reduces visibility on roads, and increases flood water risks (Mclean, 2010; Payne and Hoxley, 2012). High costs due to *R. japonica* deleterious effects (e.g., £165,609,000 per year in Great Britain; Williams et al., 2010) and management (e.g., €32,300,000 per year in

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* Corresponding author.
E-mail address: alice.michelot@univ-lorraine.fr (A. Michelot-Antalik).

Germany, including *R. japonica*, *Fallopia sachalinensis*, and *Polygonum wallichii*; Reinhardt et al., 2003) are crucial issues for managers of public or private spaces, which require more efficient control methods. Instead of eradication, the limitation of *R. japonica* spread and growth seems to be an achievable goal for reducing the impact of invasive species at a low cost (Panetta and Gooden, 2017).

To date, chemical, biological, and mechanical methods have been developed to limit the invasion of *R. japonica*. Chemical control is no longer widely used because of legal restrictions on herbicide use (e.g., Labbé's law for French cities) and limited long-term efficacy due to the risk of regrowth (Lawson et al., 2021). Biological methods use living organisms to control the development of invasive species. Among these methods, repeated grazing by goats depletes rhizomal reserves, reducing the percentage of the plant cover, survival, stem height, and biomass of *R. japonica* (Bozec et al., 2019; Brabec and Pyšek, 2000; Lerch et al., 2016). However, repeat grazing may present a risk of metallic trace element accumulation in animals on certain soil-contaminated sites (Lerch et al., 2022). Other methods introduce insects based on the "enemy release" hypothesis, which states that the success of the invasion is due to the absence of natural predators (Keane and Crawley, 2002). For example, the sap-sucking insect *Aphalara itadori* (Hemiptera: Psyllidae) was introduced to damage the plants of *R. japonica* in the United Kingdom, Canada, and the United States. This insect appears to be effective, as it is host specific (Shaw et al., 2009) and reduces *R. japonica* biomass (Grevstad et al., 2013). However, the establishment of *Aphalara itadori* could be limited by predation, foliage age (Jones et al., 2020), or humidity and temperature (Fung et al., 2020). Mechanical methods consist of excavating rhizomes or reducing *R. japonica* biomass. Excavation is drastic and requires substantial financial resources. The rapid detection and manual unearthing of rhizome fragments that have recently been rooted can be economically advantageous but unsustainable in highly invaded ecosystems (Rouleau et al., 2023). Many alternative methods exist (Collard et al., 2018), such as tarping installation (Martin et al., 2024), which inhibits plant photosynthesis but can also lead to soil impoverishment.

Among these methods, mowing appears to be a suitable method when consistently applied over several years at a sufficiently high frequency (McHugh, 2006) and adapted to management constraints. However, careful residue management is required to prevent regrowth, as rhizome fragments of *R. japonica* measuring 1 cm in length and weighing 0.7 g are capable of regeneration (Bailey et al., 2009). These mechanical treatments are essential for depleting plant reserves at low costs. However, their efficiency depends on the environmental context (Martin et al., 2020a) and does not seem sustainable for restoring the functioning of ecosystems. Indeed, after the cessation of these mechanical interventions, *R. japonica* can regrow, especially on bare ground. In this context, we seek to control *R. japonica* by combining mowing with a natural mechanism, namely, competition between plant species. A desired consequence is the limitation of invasive regrowth and the reduction of human intervention, leading to lower economic costs. Consequently, we aim to screen plant communities that could be used in restoration ecology to limit the establishment of *R. japonica* after mowing. Thus, we used the concept of limiting similarity, which predicts that species occupying the same ecological niches and using the same resources will enter into competition, thereby limiting coexistence (Loreau, 2000; Macarthur and Levins, 1967; Shea and Chesson, 2002). An essential first step is to select restoration plant species according to the following criteria: native, non-invasive, adapted to the habitat and its pedoclimate and to management (e.g., frequent mowing), competitive for sustainable development against the target invasive species, and low cost to install. Some studies have tested promising restoration species against *R. japonica* or *R.* x *bohemica* with one tree species, such as *Salix sp.* (Delbart et al., 2012; Dommanget et al., 2015, 2019), due to their competitive characteristics for light, water, nutrients, or *Sambucus ebulus* (Christina et al., 2015), which has allelopathic potential. *Salix viminalis* decreased the ramet density, height, and biomass of *R. japonica*

in semi-controlled mesocosms (Dommanget et al., 2019). Only Skinner et al. (2012) test a seeding from a multispecies native mix of grasses and shrubs for restoration without repeated mowing in a US floodplain. They showed contrasting results in the establishment of sown species, highlighting the need to deplete *R. japonica* reserves before plants establishment. Overall, there is a lack of scientific references on methods combining repeated mowing and multispecies seeding. In an original way, our study analyzed both the effects of a method combining repeated mowing and competition on *R. japonica* growth and the evolution of restoring plant communities with inter-annual *in-situ* monitoring over five years. This type of study can improve our understanding of the effect of plants invasion on resident communities (Fried et al., 2019) and assess the effectiveness of the restoration method.

Against this backdrop, our research questions were as follows: (1) What are the individual and joint effects of mowing and plant competition on the growth of *R. japonica*? (2) What are the interannual dynamics of plant communities in the different restored plots? (3) What are the establishment dynamics of the sown species? Our strategy involved two invaded experimental urban sites at which *R. japonica* growth variables were measured over three years. The study included different plant community combinations to increase the complementarity of niches and to identify efficient species for restoration. Finally, the five-year study allowed access to the sustainability of the planned restoration solutions.

2. Materials and methods

2.1. Study site

The study was conducted in the city of Laxou in northeastern France. Its climate is semi-continental, with a mean annual temperature of 10.6 °C and a mean annual precipitation of 897 mm (from 1991 to 2021, "Climate Data for Cities Worldwide," n.d.). The experimental sites comprised two restoration sites (1 and 2) invaded by *R. japonica* that were easy to access and selected in consultation with green space managers. Site 1 extended over a flat area of 238 m^2 (48°626′N, 6°132′E, 321 m a.s.l.). Site 2 was separated by a road from Site 1 and covered an area of 110 m^2 on the edge of a wood (48°687′N, 6°132′E, 324 m a.s.l.). Restoration processes aimed at limiting *R. japonica* expansion by monthly mowing and establishing concurrent plant cover at sites 1 and 2. Moreover, two control plots were selected near the restoration sites: a plot (M) mowed at the same frequency as the restoration sites and a plot (NM) that was not mown (48°687′N, 6°132′E, 325 m a.s.l.). Soil samples from the two first horizons (to a depth of 43 cm) were collected at sites 1 and 2 in December 2014 to measure total C and N concentrations on 20 mg of dry soil according to the Dumas method (elemental auto-analyzer Flash EA 1112 series; Thermo Fisher Scientific, Courtaboeuf, France). Additional soil samples were collected in April 2015 from a depth of 0–20 cm and transferred to the Soil Analysis Laboratory (LAS Arras, INRAE Lille, France) for measurements of soil texture (NF × 31–107), soil organic matter (NF ISO 10390), pH (NF ISO 10693), active limestone content (NF × 31–130), cation exchange capacity Metson (NF × 31–130), and nitrate and ammoniacal nitrogen contents (INRAE method from an extract 1/10 at KCl 0.5 mol L^{-1}). Table 1 reports soil analyses.

2.2. Plot management of restoration sites

Sites 1 and 2 were regularly managed from 2012 to 2014 by green space managers to test the initial methods of restoration. During this period, site 1 was frequently mown, and grass species were sown to cover the bare soil. The *R. japonica* at site 2 was treated by thermal action or spraying with sodium chloride to slow development. The efficiency of these tests was mixed, not precisely quantified. In May 2015, the ramet density of *R. japonica* was 35 ± 3 and 51 ± 7 ramets m^{-2} (mean ± SE), respectively, for sites 1 and 2, slightly lower to that of the control plots M and NM, which was 59 ± 3 and 45 ± 3 ramets m^{-2}

Table 1
Physico-chemical soil analyses of the study sites (1 and 2) for four restoration plots (A, B, C, D). C/N: ratio of carbon to nitrogen (mean (SE)); texture (CL: clay loam, L: loam); SOM: soil organic matter content; nitrate: nitrate nitrogen content; ammonium: ammoniacal nitrogen content, CEC: cation exchange capacity Metson.

Site	C/N	Plot	Texture	pH	SOM (%)	Nitrate (mg kg^{-1})	Ammonium (mg kg^{-1})	Total limestone (g kg^{-1})	Active limestone (g 100 g^{-1})	CEC (cmol$^+$ kg^{-1})
1	19.2	A	CL	8.06	34.9	40.6	5.61	145	3.37	21.5
	(1.5)	B	CL	8.04	46.4	48.9	6.18	145	3.68	22.3
2	25.5	C	CL	8.08	32.8	48.5	5.42	152	3.62	18.4
	(1.7)	D	L	8.09	29.9	27.6	3.97	133	2.81	16.2

(mean ± SE), respectively. Hence, the management from 2012 to 2014 may have slightly reduced *R. japonica* growth, though the ramet density remained high.

Our scientific experiment began in March 2015. We conceptualized a spatial design to test four plots easily identifiable by managers with different plant compositions: plots A and B for site 1 and plots C and D for site 2 (Fig. 1). Various herbaceous species (i.e., *Medicago sativa* L., 1753, *Schedonorus arundinaceus* (Schreb.) Dumort., 1824, *Dactylis glomerata* L., 1753, *Trifolium pratense* L., 1753, and *Hypericum perforatum* L., 1753) were sown by broadcasting on restoration plots A, B, C, and D. Each 50-cm rhizome of *Symphytum* x *uplandicum* "Bocking 14" was established, and shrub species (*Rubus idaeus* L., 1753, and *Betula pendula* Roth, 1788) were also established to shade *R. japonica*. The shrubs were planted in spaced rows to facilitate mowing. The choice of restoration species was based on their acclimation to soil and climatic conditions, their resistance to mowing, and their competitive strategy, as reported in the literature and plant databases. Fabacea *M. sativa* and *T. pratense* promote soil nitrogen accumulation because the nutrient cycle can be altered by the presence of *R. japonica* (Dassonville et al., 2008). Poaceae *S. arundinaceus* and *D. glomerata* are easily sown species in grassland environments that have been highly productive for several years. *Symphytum* x *uplandicum* "Bocking 14" is a species that reproduces only by vegetative propagation and rapidly covers soil.

Monthly complete mowing (i.e., *R. japonica* and the herbaceous cover) was conducted each year between March and October in 2015, 2016 and 2017 on restoration plots with a flail mower and the removal of mowed aboveground plant material. Subsequently, the selective mowing of stems of only *R. japonica* was conducted in June and September 2018 and in August 2019 using manual pruning shears without the removal of the mowed *R. japonica.*

2.3. Growth analysis

Growth measurements of *R. japonica* were taken the day before monthly mowing from May to July 2015, from May to August 2016, and from April to July 2017 on the control (M and NM) and restoration plots (A, B, C, and D). Three 0.25 m^2 quadrats were spatially distributed to represent disparate areas of *R. japonica* on each plot at each sampling date. They were spread across the entire plot, consistently occupying the same areas but not truly permanent. However, we considered the average values for several individuals and quadrats to minimize bias in relative growth calculations. We measured the specific leaf area (SLA, the ratio of the leaf area to the leaf dry mass in mm^2 mg^{-1}), plant height, plant stem diameter, and ramet density on each quadrat. The SLA was measured on the two highest fully expanded leaves per plant of *R. japonica* in four plants (n = 8), according to Perez-Harguindeguy et al. (2013). The leaf area was measured in the laboratory with a planimeter (LI-3000C) after field sampling. The leaf dry mass was weighed after a
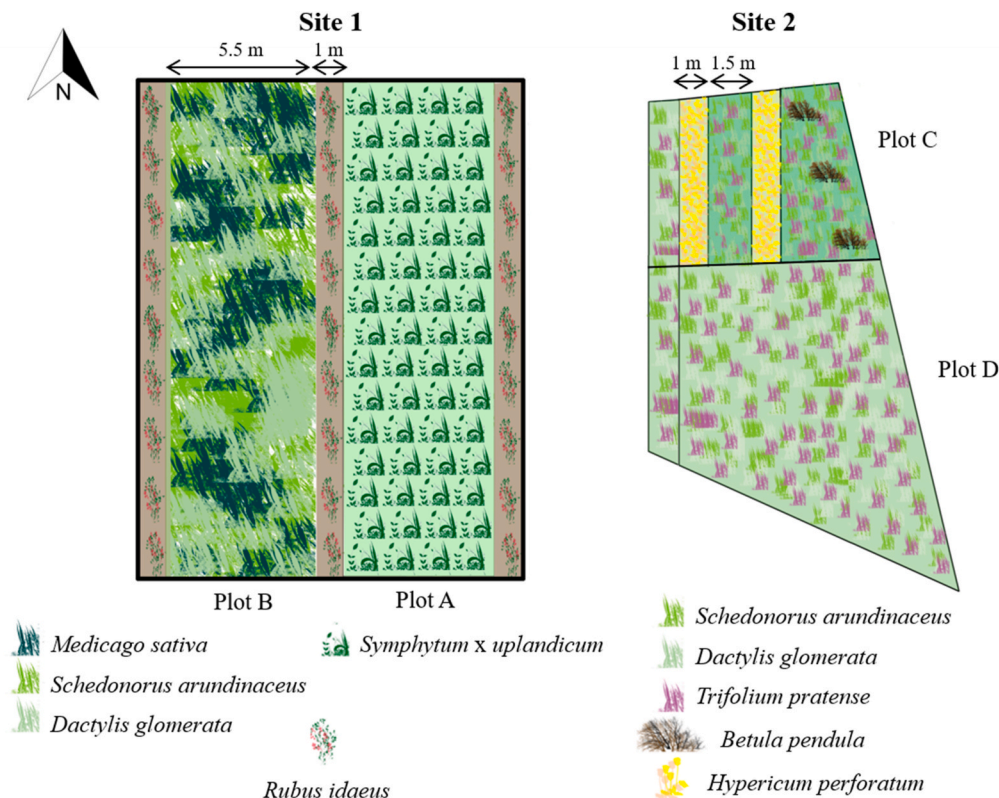
Fig. 1. Experimental design of restoration plots A, B, C, and D.

minimum of 72 h drying in an oven at 60 °C.

The height of each plant in the quadrat was measured from the base of the stem to the terminal bud or by stretching the highest leaf if it was higher than the bud using a graduated meter to the nearest centimeter. The plant stem diameter was measured at the first node with a caliper to the nearest millimeter. The daily height growth (cm day^{-1}) or daily diameter growth (mm day^{-1}) was calculated for each mowing interval as follows: $(X_{t2} - X_{t1})/(t_2 - t_1)$, where X_{t2} is the plant height or diameter before mowing at each date t_2, X_{t1} is the plant height or diameter at mowing fixed to 0, t_2 is the measurement Julian day, and t_1 is the previous mowing Julian day. Ramet density was the total number of stems per quadrat multiplied by 4 to obtain the number of stems per square meter.

2.4. Vegetation surveys

Vegetation surveys were conducted the day before the monthly mowing from May to July 2015, from May to August 2016, from April to July 2017, in June 2018, and in July 2019 on the restoration plots A, B, C, and D. The soil of the controls M and NM was only covered by *R. Japonica* and bare soil. Six 0.25 m^2 quadrats were spatially distributed to represent vegetative heterogeneity on each plot at each sampling date. The percentage cover of each plant species on each quadrat was estimated to the nearest 5%, including the bare soil. The plant strategies—competitive (C), ruderal (R), and stress (S)—were selected for each species according to Grime (1974), including competitive plants of types C, C/CR, C/CSR, C/SC, CR, CR/CSR, or CS. The mean percentage of competitive plants in each plot per year was calculated from the plant species abundance of vegetation surveys.

2.5. Statistical analyses

Statistical analyses were performed with R Studio Version 4.2.0. For growth analyses, we quantified the effect sizes of mowing and plant competition using calculations of Cohen's *d* (Cohen, 2013) with the "effsize" package for the years 2015, 2016, and 2017 separately to observe the magnitude of the "plot" and "year" effects. The effect sizes of mowing were calculated by comparing the growth variables (i.e., height growth, diameter growth, SLA, and ramet density of *R. japonica*) measured on M with those measured on NM. The effect sizes of competition were calculated by comparing the growth variables measured on the restoration plots A, B, C, and D with the growth variables measured on M. The effect sizes of both mowing and competition were calculated by comparing the growth variables measured on restoration plots with those measured on NM.

For vegetation surveys, we performed principal component analysis (PCA) using the "FactoMineR" package to compare plant community compositions in different restoration plots between years. For this analysis, we used the percentage cover of each plant species in each plot for all dates from 2015 to 2017.

We compared the mean percentage cover of competitive plant species, *R. japonica*, and bare soil between years, using Kruskal–Wallis tests because the data were not normal (Shapiro test) or heteroscedastic (Bartlett test), followed by the Wilcoxon test with Bonferroni corrections to compare pairs of means.

Statistical analysis for the repeated measures of growth variables was performed using the mixed procedure of SAS (Version 9.4, SAS Institute, Cary, USA). The mixed model included the plot (n = 6), day of measurement (n = 11), and plot-by-day interaction as fixed effects, the quadrat (n = 3 per plot) as a random effect, day as a repeated measure, and spatial power covariance structure. Logarithmic transformations were used when needed to comply with the assumptions of normality and the homoscedasticity of residuals. When transformations were needed (height growth, diameter growth, and ramet density), the means and standard errors of the mean (SEM) were estimated from untransformed values, whereas *p*-values reflected the statistical analysis of

transformed data. Significance was declared based on Tukey's test at *p* < 0.05, and trends were considered at 0.05 < *p* < 0.10. If the plot-by-day interaction was significant, the SLICE option was used to compare plot differences on each day of measurement. The values reported are arithmetic means and SEM.

3. Results

3.1. Effects of mowing

The effect sizes of mowing on height growth were largely negative for all years (from −0.90 to −0.77; Fig. 2). The diameter growth was slightly lower in 2016 (−0.21) compared to the control NM, whereas it was similar to the control NM (centered on 0) in 2015 and 2017. The effect sizes of mowing on SLA (from 0.61 to 0.95) and ramet density were highly positive for all years (from 1.83 to 1.84), except in 2017 for ramet density, for which Cohen's *d* did not diverge from 0.

Considering the three years, the plot (*p* < 0.001), day (*p* < 0.001), and interaction plot x day (*p* < 0.01) had significant effects on the four growth variables (Table 2). Mowing notably lessened the daily height growth (2.15 to 1.28 cm d^{-1}: -40%, *p* < 0.001), increased the SLA (22.3 to 28.8 mm mg^{-1}: +29%, *p* < 0.001), and increased the ramet density (71 to 110 ramets m^{-2}: +55%, *p* < 0.001) but had no significant effect on the daily growth diameter.

3.2. Effects of plant competition

Overall, the effect sizes of plant competition on SLA were approximately 0 (Fig. 2). The SLA was less in 2015 for plots A (−0.50) and C (−0.53) compared to the control plot M. The effect sizes of competition for height and diameter growth were negative overall for all restoration plots. The height growth was lower for plots A (−0.29; −0.44) and C (−0.46; −0.44) in 2015 and 2016, respectively, and for plot D (−0.46; −0.59; −0.40) in 2015, 2016, and 2017, compared to the control M, whereas it was similar to the control M (approximately 0) for all the years of plot B. The diameter growth was lower for plots B (−0.19), C (−0.33), and D (−0.46) in 2015, for all plots in 2016 with large effect sizes (between −0.80 and −0.99), and for plot D only in 2017 (−0.26) compared to the control M. The ramet density was mostly less for plots A (−1.31, −1.64, and −1.75) and B (−1.43, −3.48, and −1.65) in 2015, 2016, and 2017, respectively, and for plot C in 2016 (−1.46) and 2017 (−1.15), with the largest effect size for plot B in 2016 compared to the control M. The effect size of competition on ramet density did not differ from 0 for plot D and plot C in 2015.

Considering these three years, competition significantly decreased the daily height growth for plots A, C and D (1.28 to 0.99 cm d^{-1}: -23%, 1.28 to 0.96 cm d^{-1}: -25%, 1.28 to 0.85 cm d^{-1}: -34% *p* < 0.001), decreased the daily diameter growth for all restoration plots (from 0.15 to 0.11 mm d^{-1}: -24% to 0.15 to 0.10 mm d^{-1}: -29%, *p* < 0.001), and decreased the ramet density for plots A, B, and C (110 to 55 ramets m^{-2}: -50%, 110 to 46 ramets m^{-2}: -58%, 110 to 74 ramets m^{-2}: -33%, *p* < 0.001, see Table 2). However, competition had no significant effect on SLA for all restoration plots and ramet density for plot D.

3.3. Combined effects of mowing and plant competition

The effects of both competition and mowing (i.e., the comparison of restoration plots vs. the control NM) on height and diameter growth were negative for all plots and the three years (see Appendix A). The effects of both competition and mowing on SLA were generally positive for all plots, except in 2015 for plot A and in 2017 for plot C, for which Cohen's *d* did not diverge from 0. The effects of both competition and mowing on ramet density were very variable between years and plots: they were positive in 2015 for plots C and D; approximately 0 in 2015 for plots A and B, in 2016 for plots A, B, and D, and in 2017 for plot D; and negative in 2016 for plot B and in 2017 for plots A, B, and C.
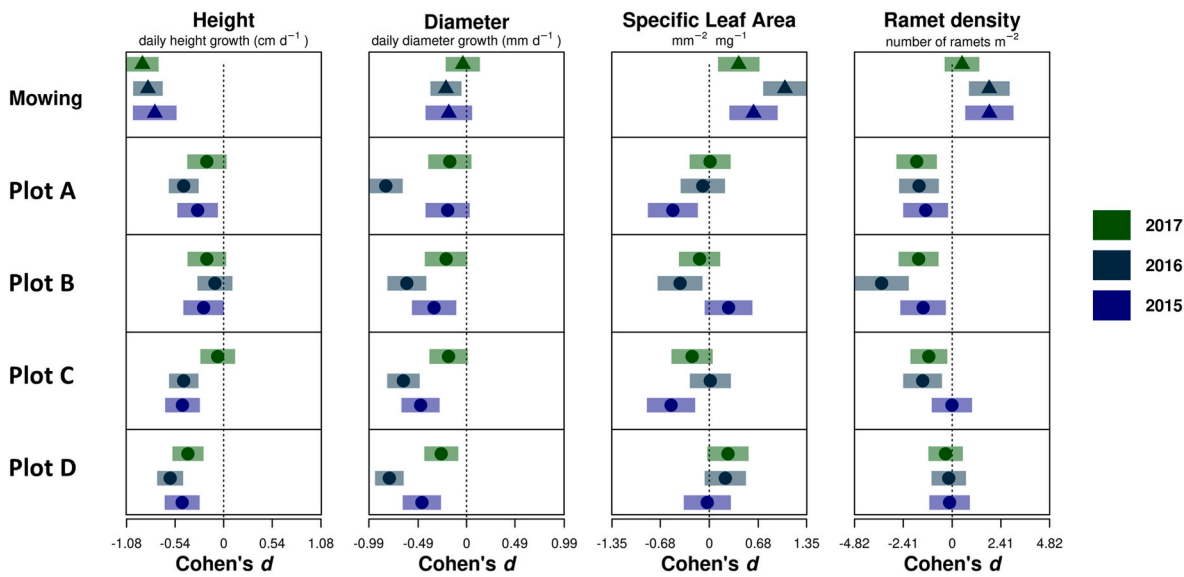
Fig. 2. Responses of daily height growth, daily diameter growth, specific leaf area and ramet density to mowing for mowing control plot (M) and to competition for plots A, B, C and D during 2015, 2016, and 2017. Triangles reflect the effect size (Cohen's d) of the mowing treatment compared to the non-mowing treatment. Circles reflect the effect size (Cohen's d) of the restoration treatments compared to the mowing treatment. Error bars indicate 95% confidence intervals.

Table 2

Effects of plot, day, and plot-by-day interactions on the means of the growth variables of *Reynoutria japonica* measured over three years (2015, 2016, 2017) on restoration plots (A, B, C, D) and control plots (mowing and non-mowing). Lower-case letters represent significant differences between plots for each variable in a column ($p < 0.05$).

		Growth variables			
		Height growth (cm d^{-1})	Diameter growth (mm d^{-1})	SLA (mm^2 mg^{-1})	Ramet density (number m^{-2})
Plot	**A**	0.99^c	0.11^b	27.2^b	55^c
	B	1.13^{bc}	0.11^b	28.5^{ab}	47^c
	C	0.96^{cd}	0.11^b	27.4^b	74^b
	D	0.85^d	0.10^b	29.8^a	100^a
	Mowing	1.28^b	0.15^a	28.8^{ab}	110^a
	Non-mowing	2.15^a	0.16^a	22.3^c	71^b
SEM		0.062	0.005	0.603	5.698
Predictors	**Plot**	$p < 0.001$	$p < 0.001$	$p < 0.001$	$p < 0.001$
	Day	$p < 0.001$	$p < 0.001$	$p < 0.001$	$p < 0.001$
	Plot * Day	$p < 0.001$	$p < 0.01$	$p < 0.001$	$p < 0.01$

Considering the three years, for all restoration plots, competition and mowing significantly decreased the height growth (from 2.15 to 1.13 cm d^{-1}: -47%, to 2.15 to 0.85 cm d^{-1}: -60%, $p < 0.001$) and the diameter growth (from 0.16 to 0.11 mm d^{-1}: -31% to 0.16 to 0.10 mm d^{-1}: -37%, $p < 0.001$, see Table 2). Competition and mowing significantly increased SLA for all restoration plots (from 22.3 to 27.2 mm^2 mg^{-1}: +22%, to 22.3–29.8 mm^2 mg^{-1}: +34%, $p < 0.001$), decreased the ramet density for plots A and B (71 to 55 ramets m^{-2}: -22%, 71 to 47 ramets m^{-2}: -34%, $p < 0.001$) and increased the ramet density for plot D (71 to 100 ramets m^{-2}: +41%, $p < 0.001$).

3.4. Intra-annual dynamics of R. japonica

The height growth of *R. japonica* tended to decrease from May to July–August in 2015, 2016, and 2017 for all plots except for an increase from May to June 2016 for plots A and B (Fig. 3a). The mean height growth values were consistently higher for the control NM compared to the restoration plots from June to July–August for each date ($p < 0.05$) except June 2016.

Concerning diameter growth, the intra-annual dynamics were relatively similar between plots with decreases from May to July–August in 2015, 2016, and 2017 for all plots except from May to June 2016 for plots A and B, where the diameter growth increased (Fig. 3b). The differences in mean diameter growth were not significant between the control NM and any restoration plot for each date except May 2016 ($p < 0.001$), July 2016 ($p < 0.05$) and April 2017 ($p < 0.05$).

The intra-annual dynamics of mean SLA diverged from that of height and diameter growths (Fig. 3c). In 2015, the SLA decreased remarkably from May to July for all plots, except plot C, where the SLA decreased slightly. In 2016, the SLA was relatively constant from May to August for all plots except the control plot NM, with a high decrease from June to July. In 2017, the SLA increased between April and May and remained constant for restoration plots, whereas it remained stable from April to July for the M control and decreased for the NM control from May to July. The mean SLA values were significantly lower for the NM control in June 2015 ($p < 0.01$), July 2016 ($p < 0.001$), August 2016 ($p < 0.001$) and July 2017 ($p < 0.001$) compared to the restoration plots.

Significant disparities in mean growth variables between dates and plots are detailed in Appendix B.

3.5. Interannual dynamics of plant communities

From 2015 to 2019, 90 plant species were identified in the four experimental plots. Total species richness over the five years was relatively similar between plots (39; 33; 42 and 34 species, respectively for plots A, B, C and D). The composition of the plot's plant communities differed progressively from 2015 to 2017 (Fig. 4a–c). In 2015, the four plot communities were slightly varied: the ellipse of plot C overlapped with other plots, and the ellipses of plots B and D also overlapped. In 2016, the communities became more differentiated, with an overlap between the ellipses of plots A and B and between the ellipses of plots C and D. In 2017, the communities were very distinct, with only a small elliptical overlap between plots C and D. This differentiation effect was highlighted by the percentage of explained variance on the first two axes of the PCA, which increased from 2015 (28.8%) to 2017 (32.6%). *Lolium multiflorum*, *Poa trivialis*, and *Trifolium pratense*; *Rumex acetosa*, *Plantago lanceolata*, and *Robinia pseudoacacia*; and *Symphytum* x *uplandicum*,
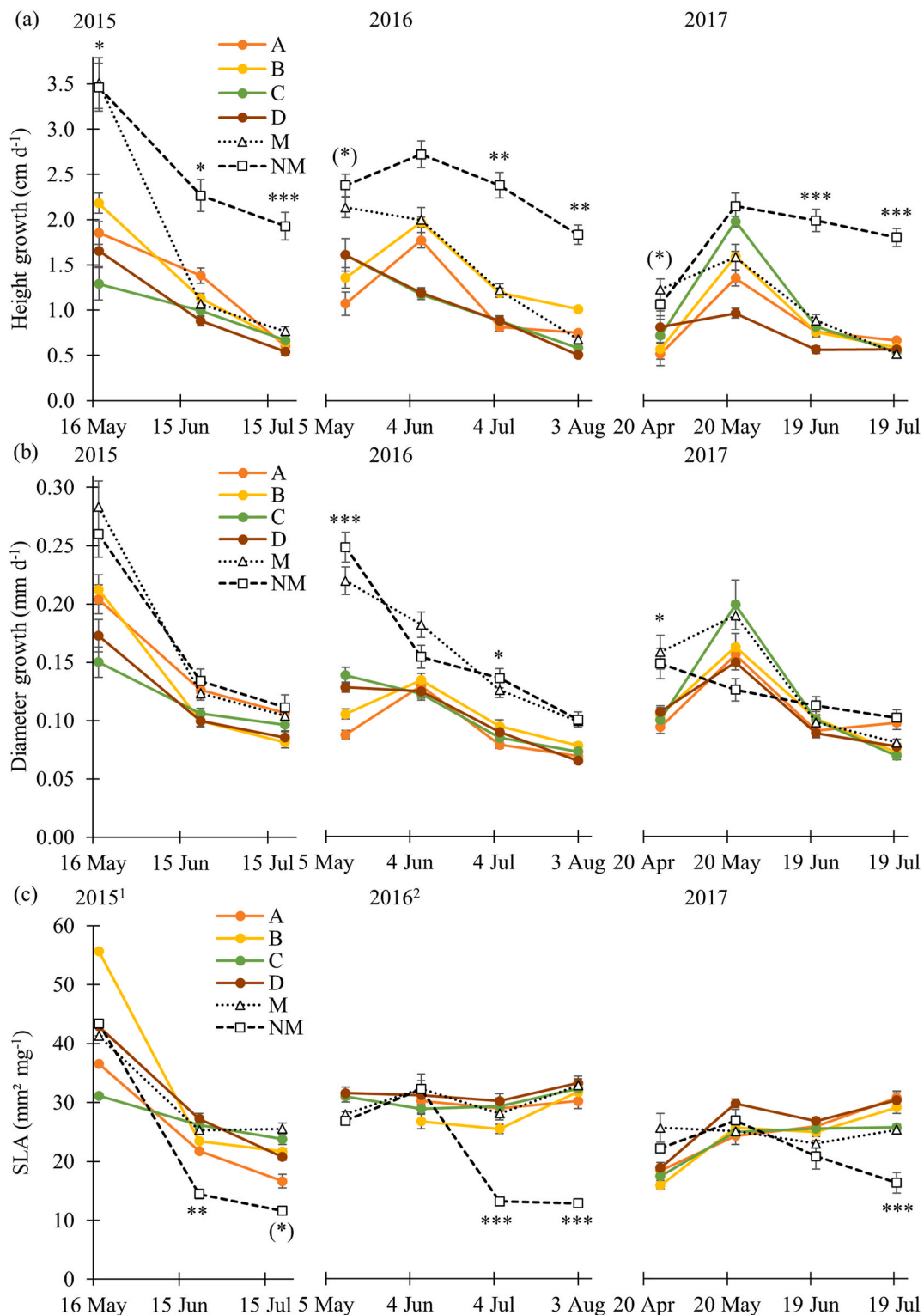
Fig. 3. Intra-annual dynamics of the (a) daily height growth, (b) daily diameter growth, and (c) SLA (specific leaf area) of *R. japonica* from 2015 to 2017 in restoration plots (A, B, C, D) and control plots (M, NM). The error bars represent ± SE. Each mean variable was compared for each date between restoration plots and the non-mowing control with the significance (*) $p < 0.10$, *$p < 0.05$, **$p < 0.01$, and ***$p < 0.001$. [1]In 2015, the dry leaf weight was measured for the sum of eight leaves per quadrat, which did not provide an SLA value for each individual. [2]In May 2016, the SLA values were not measured for plots A and B due to unplanned mowing.

Taraxacum sp., and *Urtica dioica* were the species that contributed most to the PCA axis in 2015, 2016, and 2017, respectively. The mean proportion of the four plots from mid-June to July ranked between 15.4% in 2015 and 38.5% in 2019 for grass plants (including Poaceae and

Cyperaceae), 66.7% in 2015 to 32.5% in 2019 for forbs, and 0.6% in 2019 to 6.5% in 2015 for legumes. Fig. 5 illustrates the vegetation evolution of site 1 between late June 2015 and early July 2019.

Grime's competitive types represented the dominant vegetation for
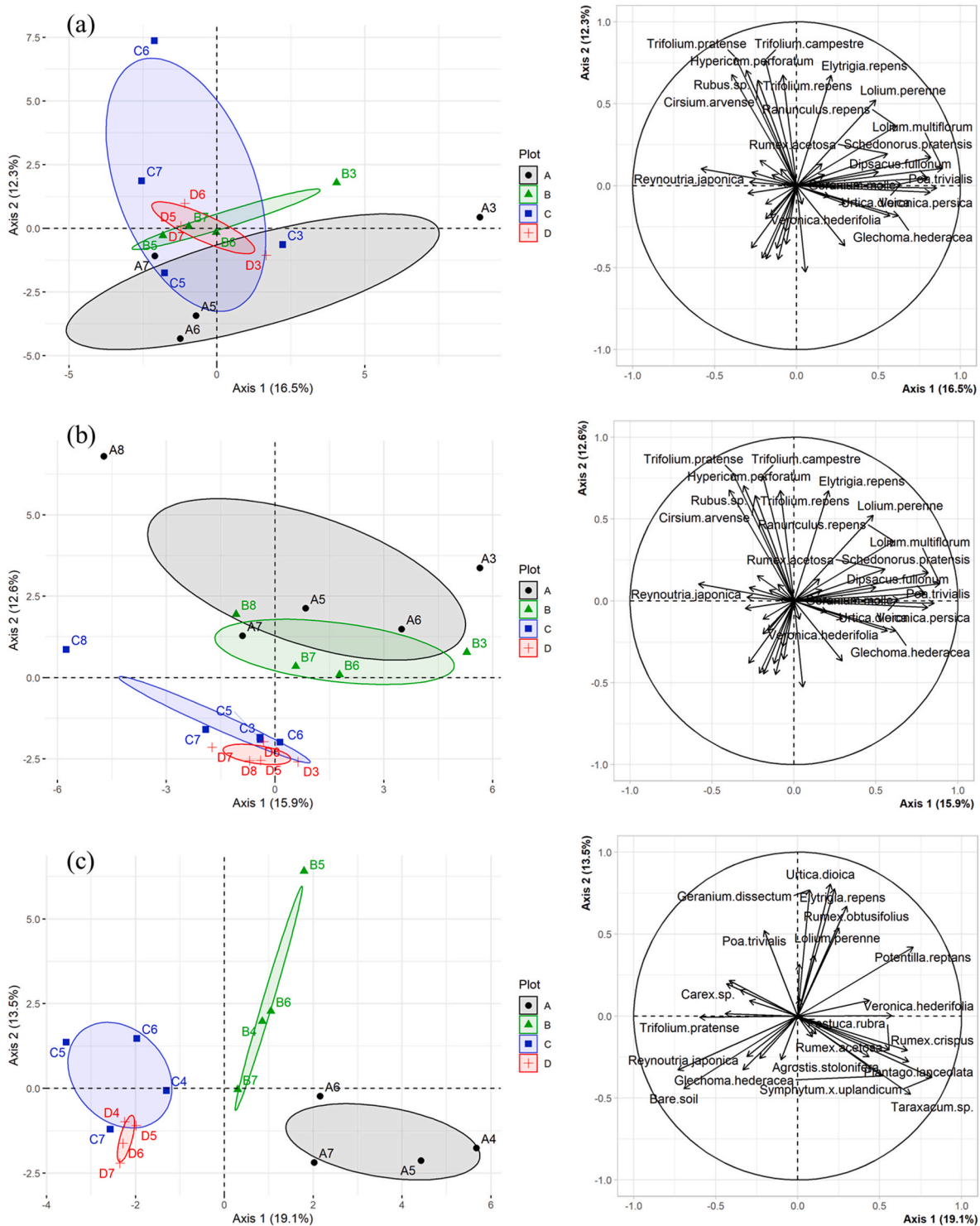
Fig. 4. The principal component analysis (PCA) of the mean plant abundance of each plot (A, B, C, D) at different sampling dates in (a) 2015, (b) 2016, and (c) 2017, including individual (plot) and variable (species) graphs. The plot numbers indicate the month of sampling (e.g., "4": April). Only the 20 most contributed species for the two axes are indicated for each variable graph.

all restoration plots during the five years (from $42.8 \pm 4.4\%$ in 2015 to $55.4 \pm 9.5\%$ in 2018, mean $\pm$ SE, see Table 3). The *R. japonica* cover was significantly lower in 2017 ($5.0 \pm 1.3\%$) than in 2015 ($19.4 \pm 3.9\%$, $p < 0.01$). The proportion of bare soil increased significantly between 2016 ($17.6 \pm 2.9\%$) and 2017 ($32.2 \pm 3.8\%$, $p < 0.05$).

3.6. Establishment of sown plant species

Among the sown species, four have been established permanently according to their ecology: *Symphytum* x *uplandicum*, *Dactylis glomerata*, *Schedonorus arundinaceus*, and *Trifolium pratense*. The cover of *S. uplandicum* progressively increased from 2015 to 2019 ($1.5 \pm 0.9\%$–24.2%, mean $\pm$ SE) in plot A (Fig. 6). *D. glomerata* was relatively abundant after its second year of establishment in three plots, with a

Fig. 5. Authors' pictures of vegetation evolution of the site 1 between late June 2015 (top) and early July 2019 (bottom).

Table 3
Means and standard errors of percentage coverage for competitive plant species (Grime types), *Reynoutria japonica*, and bare soil from 2015 to 2019 in all plots. Lower-case letters represent significant differences between years for each variable in a column ($p < 0.05$). [1]Mean comparison tests were not administered for the 2018 and 2019 data because only one sampling date was conducted in these years (n = 4).

| Year	Competitive plants		R. japonica		Bare soil	
	Mean	SE	Mean	SE	Mean	SE
2015	42.8[a]	4.4	19.4[a]	3.9	17.7[ab]	4.1
2016	55.6[a]	4.1	9.2[ab]	2.1	17.6[a]	2.9
2017	48.8[a]	4.5	5.0[b]	1.3	32.2[b]	3.8
2018[1]	55.4	9.5	11.7	6.1	22.3	4.3
2019[1]	55.0	8.0	6.2	2.9	28.3	4.5

maximum of 26.5 ± 6.5% in 2017 for plot B, 14.8 ± 1.4% in 2016 for plot C, and 30% in 2018 for plot D. The *S. arundinaceus* cover was highest in 2019 for the three plots, with 14.2%, 10.0%, and 5.8% for plots B, C, and D, respectively. *T. pratense* was relatively abundant only in the second year after sowing in plot C (23.8 ± 8.0%) and less abundant in plot D (7.7 ± 3.9%). *Medicago sativa* was not established in plot

B. *Rubus idaeus* did not establish well, with a gradual loss over the years, reducing the initial pool to a quarter of the species planted (data not shown). *Hypericum perforatum* plants lasted one year after their implantation on plot C (data not shown).

4. Discussion

4.1. R. japonica development was affected by mowing and plant competition

Regardless of competition, frequent mowing increased *R. japonica* SLA (+29%) from 2015 to 2017. These effects suggest potential changes in carbon allocation patterns toward leaves as a response to mowing and a shift to an even more resource-acquisitive strategy. Indeed, SLA positively correlates with the photosynthetic and relative growth rates (Cornelissen et al., 2003). This strategy of carbon acquisition coupled with an early phenology (Beerling et al., 1994) ensures the efficient capturing of light and carbon entry for biomass production in the plant community (Dommanget et al., 2013). Mowing also largely decreased the height growth of *R. japonica* from 2015 to 2017 (−40%), with an intra-annual reduction from May to July–August, in agreement with Rouifed et al.'s (2020) findings, where one cut every four weeks reduced
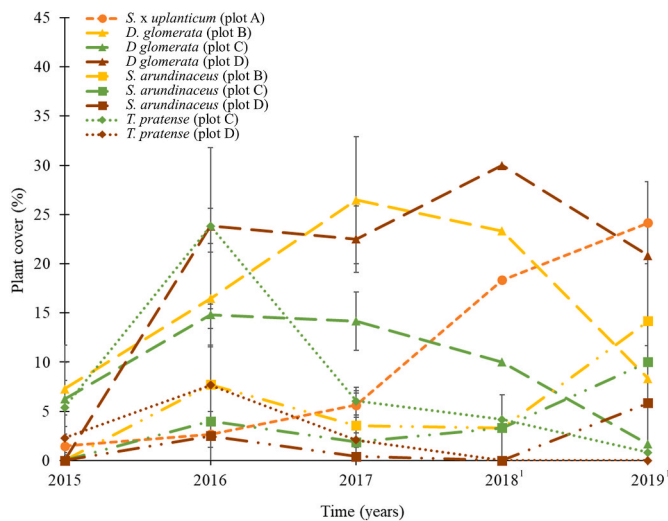
Fig. 6. Means of percentage cover for the sown species: *Symphytum* x *uplandicum*, *Dactylis glomerata*, *Schedonorus arundinaceus* and *Trifolium pratense* from 2015 to 2019 on each plot (A, B, C and D). [1]No value was calculated for SE in 2018 and 2019 because only one sampling date was conducted. The error bars represent ± SE.

the maximal height of *R. sachalinensis* and *R.* x *bohemica* by 75%. Mowing increased the ramet density (+55%) in 2015 and 2016, which contradicts previous studies observing a decrease in ramet density (Delbart et al., 2012; Rouifed et al., 2020) or no effect of mowing (Martin et al., 2020a) during one-year experiments. *R. japonica* could respond to frequent mowing in the first two years by using the reserves stored in its rhizomes to enable buds to break their dormancy and generate new stems in large numbers (Schnitzler and Muller, 1998). This effect may disappear with the progressive depletion of reserves in the third year. Apart from SLA, height growth, and ramet density, mowing did not affect diameter growth, suggesting a constant carbon allocation to radial growth, regardless of the perturbation frequency.

Competition decreased the height growth (−12% to −34%) and diameter growth (−24% to −29%) and had no significant effect on mean SLA over the three years. These observations may highlight the trade-off between the carbon allocation to leaves for resource acquisition due to the competition and stem biomass for *R. japonica*. Delbart et al. (2012) and Dommanget et al. (2019) also observed a decrease of the stem biomass and height on *R. japonica* with competition from *Salix* sp. Generally, the competition effect could be slightly impacted by the observed difference in ramet density between plot M and restoration plots in 2015 when our experiment beginning.

The increased effect of mowing on the ramet density of *R. japonica* stems in 2015 and 2016 was a negative result for *R. japonica* management, but the competition of restoration plants reduced this effect for most plots (−9% to −58%). Hence, this study stresses the importance of plant restoration communities limiting the adverse effects of the mechanical control of *R. japonica*, such as mowing.

4.2. Most competitive sown species were well established and complementary to limit R. japonica development

The establishment of seeded herbaceous species was successful in our study because four species were permanently established according to their ecologies and the environmental conditions of the experimental plots: *Symphytum* x *uplandicum, Dactylis glomerata, Schedonorus arundinaceus*, and *Trifolium pratense*. *S.* x *uplandicum* appeared to be a very interesting species for restoration because its establishment was gradual and sustainable, with a high cover proportion in 2019. The longevity of the three grassland-sown species is consistent with what is commonly observed in temporary agricultural grasslands (Deraedt et al., 2014).

Therefore, as in our study, *T. pratense* is a pioneer species with a fast establishment but a life cycle lasting a maximum of four years (Sakanoue, 2002). *D. glomerata* showed a fast establishment with a high cover from 2016 to 2018 but a decline in 2019 due to its characteristics: a medium speed of establishment and high productivity after three years (Deraedt et al., 2014). *S. arundinaceus* was well established in 2019, following a slow establishment but high productivity after three years. These three species seem complementary in terms of temporal niches and appear efficient in ensuring competition against *R. japonica*. Only *Medicago sativa* was not established despite being established with its *inoculum*. Two reasons could explain this observation. First, plot B had a moderate fertility (C/N ratio of 19.2 ± 1.5, mean ± SE), and *M. sativa* is a plant species with quite high nutrient requirements. Second, plot B was mown after April every year, which could prevent *M. sativa* from reproducing because it is a rather late-flowering species. The establishment of woody species, such as *Rubus idaeus* and *Hypericum perforatum*, was also less successful, probably due to the properties of the soils, which were not fertile enough and had many stones and drying conditions.

4.3. Plant communities showed interannual dynamics in which R. japonica declined progressively

Plant communities comprised mesophilous grassland species, mainly split between grass and forbs, with a very low proportion of legumes in June–July from 2015 to 2019. In addition to the ruderal strategy, the species were mainly competitive and were thus able to efficiently capture resources despite frequent perturbations (i.e., mowing). This community strategy can be explained by the presence of *R. japonica*, which generated a high level of competition and emitted allelopathic compounds that could decrease the growth of native plants (e.g., Moravcová et al., 2011; Murrell et al., 2011). At the early beginning of the experimental treatments (in 2015), the plant communities of the plots were relatively similar, probably because invasive species generate ecosystem homogenization (McKinney and Lockwood, 1999). After three years of restoration by mowing and competition, plant communities evolved in a quite different way. This heterogenization is probably due to the gradual decline of *R. japonica* (Siemens and Blossey, 2007). The differentiation of communities was not only based on sown species, as demonstrated by the PCA axes characterized by additional species that arrived spontaneously. Restoration plants that were sown occupied bare soil after mowing, preventing the recolonization of *R. japonica* and promoting a facilitation process that enabled the establishment of other plants. Yet, even if communities showed different evolutions in their compositions, they had the same level of species richness over the past five years. Combining mowing and plant competition seems to be an interesting strategy to limit *R. japonica* development while enhancing ecosystems' resilience.

4.4. Recommendations for restoration methods to limit R. japonica invasions

This is a local study, and invasive restoration methods must be adapted to each environmental context to find the best solution. The restoration methodology adopted in this study allows managers to make appropriate decisions aimed at reducing the impact of *R. japonica* on ecosystems. Based on the feedback from our other monitored sites (Tehranchi unpublished data), it appears crucial not to leave untreated stands of *R. japonica* near restoration sites for the method to be fully effective. Monthly mowing from May to September led to a height growth decrease for the three years in this study. Mowing can be carried out using a flail mower, which cuts plants into small fragments that can be collected and exported to prevent regrowth. *R. japonica* should be cut below the first node and may not exceed 1 m in height to ensure optimal mowing and prevent fragment dispersion. Mowing costs varied according to territory management, topography, and *R. japonica* ramet

density. These costs are estimated to be between €50–70 h^{-1} without a recovery system and between €120–150 h^{-1} with a recovery system (Collard et al., 2018). The exhaustion of *R. japonica* can be carried out using other methods, such as pasture or tarping cover (Martin et al., 2024). In our study, exhaustion may have partially begun in 2012 with the initial treatments. This step is essential during certain years before the establishment of competing plant cover. Plant competition can also take place naturally by recolonizing the surrounding vegetation according to diversity. However, in this case, the ecosystem takes longer to restore, leading to a higher regrowth probability for *R. japonica*. The selection of plant restoration species requires analyzing the pedoclimatic conditions of sites and choosing native perennial species adapted to soil, climate, competition, and resistance to mowing. In our study, *S. x uplandicum* and the herbaceous mixing of *D. glomerata*, *S. arundinaceus*, and *T. pratense* seemed adapted to our site conditions. These sown species are low cost, about €200 ha^{-1} (density of 30 kg seeds ha^{-1}). As the cost of other species, such as shrubs, could be higher and their successful implementation less guaranteed, managers should consider their establishment according to ecosystem characteristics. The restoration method proposed in this study enabled the establishment of mesophilous grassland vegetation, which was not expensive. A decrease in mowing frequency after 2018 allowed the establishment of late-mowing species, such as *Centaurea jacea*, which would have been impossible at the start of mowing in 2012. In 2024, *R. japonica* had not yet regained its 2015 density on our restoration sites, and our strategy appears to effectively limit reinvasion sustainably. It will be necessary to assess whether *R. japonica* does not massively recolonize the sites in the absence of management over the next few years.

5. Conclusion

Our study shows that the coupling of timely and mechanical interventions and ecological methods based on the reasoned choice of plant species competing with invasive species seems ecologically relevant, technically feasible, and economically viable. The effectiveness of the method to prevent the reinvasion of *R. japonica* appears relatively sustainable, as was still apparent in 2024. Such inter-annual *in situ* monitoring of ecosystems, which had not yet been carried out until now, makes it possible to propose recommendations to managers having to deal with the colonization of the environment by invasive species such as *R. japonica*. This method can be deployed within transportation infrastructures, such as roads and railroads, or within easily accessible terrestrial ecosystems, contingent upon management priorities and the environmental context.

CRediT authorship contribution statement

Alice Michelot-Antalik: Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Alan Kergunteuil:** Writing – review & editing, Formal analysis. **Léa Genty:** Writing – review & editing, Formal analysis. **Paul Montagne:** Project administration, Methodology, Funding acquisition, Conceptualization. **Christophe Robin:** Writing – review & editing. **Mitra Tehranchi:** Writing – review & editing, Formal analysis, Data curation. **Sylvain Lerch:** Writing – review & editing, Validation, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Paul Montagne reports financial support was provided by Fondation de France. Paul Montagne reports financial support was provided by Conseil Général Meurthe et Moselle. Paul Montagne reports financial support was provided by DREAL Grand Est. Alice Michelot-Antalik reports was provided by Synergie Plantes Invasives Grand-Est - SPIGEst. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Appendix A

Responses of, daily height growth, daily diameter growth, specific leaf area and ramet density to competition and mowing for restoration plots A, B, C and D during 2015, 2016 and 2017. Circles reflect the effect size (Cohen's *d*) of the restoration treatments compared to the non-mowing treatment. Error bars indicate 95% confidence intervals.

Appendix B

Effects of the plot, day, and plot-by-day interaction on the least square means of growth variables of *Reynoutria japonica* measured for each date on the three years (2015, 2016, and 2017) on restoration plots (A, B, C, D) and control plots (mowing and non-mowing). Lower-case letters represent significant differences between plots for each growth variable and date in a column ($p < 0.05$). nd: Not determined.

Growth variable	Year 1 (2015)			Year 2 (2016)				Year 3 (2017)					p-value		
Plot	16 May	15 June	15 July	5 May	4 June	4 July	3 August	20 April	20 May	19 June	19 July	SEM	Plot	Day	Plot * Day
Height growth (cm d⁻¹)															
A	1.84[b]	1.39[b]	0.60[b]	1.05[c]	1.77[b]	0.91[b]	0.83[bcd]	0.53[b]	1.36[bc]	0.81[b]	0.66[b]	0.194	<0.001	<0.001	<0.001
B	2.22[b]	1.15[bc]	0.66[b]	1.34[c]	1.95[ab]	1.25[b]	1.03[b]	0.64[b]	1.51[ab]	0.75[b]	0.61[b]				
C	1.41[c]	0.95[bc]	0.68[b]	1.53[bc]	1.24[c]	0.90[b]	0.59[cd]	0.79[b]	2.01[ab]	0.86[b]	0.51[b]				
D	1.61[bc]	0.87[c]	0.53[b]	1.51[bc]	1.14[c]	0.90[b]	0.48[d]	0.78[b]	0.95[c]	0.59[b]	0.57[b]				
Mowing	3.47[a]	1.06[bc]	0.77[b]	2.10[ab]	2.00[ab]	1.27[b]	0.68[bcd]	1.28[a]	1.57[ab]	0.99[b]	0.59[b]				
Non-mowing	3.47[a]	2.32[a]	1.93[a]	2.32[a]	2.80[a]	2.41[a]	1.83[a]	1.14[a]	2.22[a]	1.98[a]	1.83[a]				
Diameter growth (mm d⁻¹)															
A	0.20[bcd]	0.13	0.11	0.09[c]	0.14	0.09[c]	0.08[b]	0.10[b]	0.16	0.10	0.10[ab]	0.016	<0.001	<0.001	<0.01
B	0.22[abc]	0.10	0.08	0.11[bc]	0.14	0.11[bc]	0.08[ab]	0.11[b]	0.17	0.10	0.08[bc]				
C	0.16[d]	0.10	0.10	0.14[b]	0.13	0.09[c]	0.08[b]	0.11[b]	0.20	0.11	0.07[c]				
D	0.17[cd]	0.10	0.08	0.13[b]	0.12	0.09[c]	0.07[b]	0.11[b]	0.14	0.10	0.08[bc]				
Mowing	0.28[a]	0.12	0.10	0.23[a]	0.19	0.14[ab]	0.10[a]	0.17[a]	0.20	0.11	0.09[bc]				
Non-mowing	0.26[ab]	0.14	0.11	0.26[a]	0.16	0.14[a]	0.10[a]	0.16[a]	0.14	0.12	0.11[a]				
SLA (mm² mg⁻¹)															
A	36.6[d]	21.8[b]	16.8[bc]	nd	30.9	29.6[a]	30.9[a]	18.8[bc]	24.8	26.5	31.4[a]	1.92	<0.001	<0.001	<0.001
B	55.7[a]	23.4[ab]	21.7[ab]	nd	27.3	26.0[a]	32.5[a]	16.2[c]	26.3	25.5	29.8[ab]				
C	31.2[e]	26.1[ab]	23.8[a]	31.7	29.5	30.0[a]	33.0[a]	17.8[bc]	25.5	26.1	26.3[ab]				
D	42.9[bc]	27.2[a]	20.8[ab]	32.3	31.9	30.9[a]	34.0[a]	19.3[bc]	30.5	27.4	31.0[ab]				
Mowing	41.3[cd]	25.3[ab]	25.6[a]	28.6	33.0	28.7[a]	33.6[a]	26.2[a]	25.6	23.5	25.9[b]				
Non-mowing	43.4[b]	14.4[c]	11.7[c]	27.5	33.0	13.4[b]	13.1[b]	22.7[ab]	27.5	21.3	16.7[c]				
Ramet density (number m⁻²)															
A	32	55[b]	75	59[b]	52[bc]	105[ab]	81[b]	32[c]	33[b]	48[b]	37[c]	18.2	<0.001	<0.001	<0.01
B	37	65[b]	59	48[b]	36[c]	49[c]	52[b]	35[c]	27[b]	57[b]	39[c]				
C	48	152[a]	84	57[b]	65[bc]	124[ab]	67[b]	44[bc]	33[b]	73[ab]	64[bc]				
D	55	132[a]	84	65[b]	92[ab]	187[a]	160[a]	65[ab]	69[a]	121[a]	67[bc]				
Mowing	59	136[a]	91	113[a]	133[a]	131[ab]	165[a]	81[a]	63[a]	107[a]	133[a]				
Non-mowing	45	53[b]	39	108[a]	77[ab]	76[bc]	69[b]	77[ab]	84[a]	83[ab]	69[ab]				

Appendix C. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2024.121818.

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