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Characterisation of Underground Organs as a Basis for Estimating Rhizome Resprouting Potential: The Case Study of Two Invasive *Reynoutria* Taxa (Polygonaceae)

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ABSTRACT

The Japanese knotweeds (*Reynoutria japonica* complex; Polygonaceae) are characterised by a highly efficient vegetative propagation. Their resprouting capacity is associated with rhizomes, whose nodal structure distinguishes them from non-regenerative roots. Knowing the distribution of both organ types is therefore a key prerequisite for eradication measures. The present study aimed to assess (i) the distribution patterns of rhizomes and roots, (ii) the resprouting capacity of rhizomes and (iii) the overall resprouting potential of *Reynoutria japonica* and *Reynoutria* ×*bohemica*. For this purpose, we characterised the underground organs of six established and undisturbed populations and carried out resprouting tests with rhizomes in a greenhouse. Our results highlighted that the rhizome biomass of both taxa is mainly concentrated in the top 40 cm of soil, although some outlying rhizome organs may be found deeper down depending on soil compaction. On average, the observed density of nodes per square metre was 2646, ranging from 1825 in compact soil to 3825 in loose soil. Conversely, roots mostly occur in deeper soil layers. The rhizome resprouting capacity was significantly explained by pith brightness, organ diameter and taxon. Based on these findings, we estimated the overall potential of resprouting nodes by linking the number and characteristics of visible rhizomes along the soil profile to their resprouting capacity. We obtained expected densities of 1981 ± 198 and 1935 ± 305 nodes/m^2 for *R. japonica* and for *R.* ×*bohemica*, respectively. We conclude with practical recommendations on incorporating preliminary rhizome depth and resprouting potential assessments into management practices to optimise resource allocation.

1 | Introduction

The Japanese knotweeds (*Reynoutria japonica* complex, currently classified under the genus *Reynoutria* Houtt.; formerly classified under *Fallopia* Adans. and *Polygonum* L.; Polygonaceae; Desjardins et al. 2023) behave as extremely invasive neophytes in many regions of the world where they have been introduced (Lowe et al. 2000). In Europe, concern has been raised over two taxa (i.e., *R. japonica* Houtt. and *R. sachalinensis* Nakai) that were imported as ornamental and fodder plants in the 19th century (Beerling et al. 1994). Meanwhile, their hybrid *R.* ×*bohemica* Chrtek & Chrtková was discovered and described in Europe (Chrtek and Chrtková 1983) where it tends to dominate in case of the presence of both parental taxa (Bímová et al. 2003, 2004; Bailey et al. 2009).

From a management perspective, the ability of Japanese knotweeds to form dense and monospecific populations (Aguilera

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et al. 2010; Hejda et al. 2009; Künzi et al. 2015; Lavoie 2017), combined with their highly efficient and plastic underground clonal growth assured by woody rhizomatous stocks and rhizomes, represents the main challenge for their control (Beerling et al. 1994; Adachi et al. 1996a; Richards et al. 2012; Zhang et al. 2016; Jones et al. 2018). Rhizomes typically extend horizontally within two meters of above-ground stems in small stands and up to 2.5 m in larger ones (Fennell et al. 2018). These rhizomes can adapt their growth form to environmental conditions, producing thick, short 'phalanx' rhizomes in full light and thin, elongated 'guerrilla' rhizomes under shade or mechanical stress (Martin et al. 2020). Additionally, the capacity to form anastomoses within the underground system enables the plant to overcome temporary resource scarcity caused by stress or disturbance by redistributing and optimising water, nutrient and carbon allocation (Beerling et al. 1994; Jónsdóttir and Watson 1997; Smith et al. 2007; Liu et al. 2016). Controlling and/or eradicating efforts should thus be informed by a comprehensive understanding of the distribution of the underground organs (Seiger and Merchant 1997; Child and Wade 2000; Jones et al. 2018; Dommanget et al. 2019).

The extant literature suggests that the underground system may extend to a depth of 1.5–2 m (Child and Wade 2000; Smith et al. 2007; Macfarlane 2011; Shaw 2013; Fennell et al. 2018), with a concentration of rhizomes in the upper soil layers (Adachi et al. 1996b; Fennell et al. 2018; Dommanget et al. 2019). Drawing on extensive field observations, Dommanget et al. (2019) distinguish between erratically exploratory rhizomes confined to the superficial soil layer and a deeper rhizomatous system that rarely reaches 1 m deep in most natural soils. Consequently, the differentiation between problematic resprouting rhizomes and roots constitutes a fundamental botanical and biological distinction (Dommanget et al. 2019; Jousson et al. 2024). Unlike roots, the rhizomes of knotweeds are characterised by the presence of a central pith and peripheral dormant buds at their nodes that enable resprouting, a capacity most pronounced during early ontogeny and diminishing across later developmental stages (Jousson et al. 2024).

In this study, we built upon the morphological and anatomical knowledge provided by Jousson et al. (2024) on the underground organs of the Japanese knotweeds with the aim of assessing (i) the distribution patterns of rhizomes and roots and (ii) the resprouting capacity of rhizomes. Based on the obtained results, we then (iii) estimate the overall resprouting potential for each of the considered knotweed taxa. To this end, six sites located in Canton Ticino (southern Switzerland) were selected, each hosting well-established, undisturbed populations of either *R. japonica* (three sites) or *R.* ×*bohemica* (three sites). At each site, excavations and soil profiles were performed to investigate the distribution and characteristics of underground organs, with particular focus on the resprouting rhizomes.

2 | Materials and Methods

2.1 | Study Area and Site Selection

The study area is situated in and around the main alluvial plain of the Ticino and Brenno Rivers in Canton Ticino (southern Swiss Alps) at elevations ranging from 200 to 450 m a.s.l. (Figure 1). The geological substrate is constituted by metamorphic crystalline rock, notably gneiss, which characterises the Alpine formations of Canton Ticino (Labhart 1992). From this bedrock, intermediate sandy loam soils with sandy deposits, gravels and pebbles are derived (Scapozza 2013; Czerski et al. 2022). The region is characterised by the Insubric climate with mild and dry winters followed by warm and stormy summers (Spinedi and Isotta 2004). The mean annual precipitation and temperature are 1806 mm and 11.9°C, respectively (climate normal 1991–2020, Meteoswiss climatological station of Magadino/Cadenazzo).

All taxa of the *Reynoutria japonica* complex can be found within the region, that is, the parental *R. japonica* Houtt. and *R. sachalinensis* (F. Schmidt) Nakai, and their hybrid *R.* ×*bohemica* Chrtek and Chrtková (InfoFlora Database 2025). *R. japonica* is widely distributed, especially in the region of Bellinzona and in the Blenio Valley in northern Ticino, whereas *R.* ×*bohemica* is more common on the Magadino plain in Central Ticino (Figure 1). In contrast, *R. sachalinensis* is only sporadically present. The present study focuses on the two most frequent *R. japonica* complex taxa in the study area, that is, the parental *R. japonica* and the hybrid *R.* ×*bohemica* (see Figure 2 for taxon identification and Mereďa Jr et al. 2019).

Sites were selected according to the following criteria: the presence of established knotweed populations with an age of at least 15 years, occupying a minimum area of 500 square metres, exhibiting undisturbed growth and occurring in soils uniformly characterised as sandy loam. Field determination of the taxa was conducted by means of the presence of trichomes (indumentum) on the veins of the lower (abaxial) side of the leaves, which are absent on *R. japonica* (developed as papillae) and long, that is, 0.1–0.3 (0.5) mm on *R.* ×*bohemica* (Alberternst and Böhmer 2011; Mereďa Jr et al. 2019). For each taxon, we selected a main study site accessible with a mechanical shovel and two ancillary sites, for a total of six study sites (Figure 1).

2.2 | Sampling Design

Figure 3 illustrates the sampling design applied during excavation activities carried out at the end of the growing season in November 2023. At both main study sites, we dug a trench measuring 100 cm in width, 440 cm in length and 100 cm in depth to study in detail the underground organ distribution of the two target taxa. To study the among-sites variability of the resprouting organs in the main rhizome-hosting layers, we additionally dug three small holes (i.e., $40 \times 20 \times 60$ cm^3 in size) at each ancillary site at 80 cm distances. The total depth of 60 cm for the holes was chosen as a compromise between workload and the need to set a priority on the distribution of rhizomes.

At the two main sites, the trenches were dug within the knotweed populations with the help of a mechanical shovel. If underground organs were still present at the bottom of the trench (i.e., 100 cm depth), further soil subunits of 20 cm in depth were manually dug with a shovel until the soil was completely devoid of any underground organs. In contrast, the $40 \times 20 \times 60$ cm^3 holes at the ancillary sites were dug manually.

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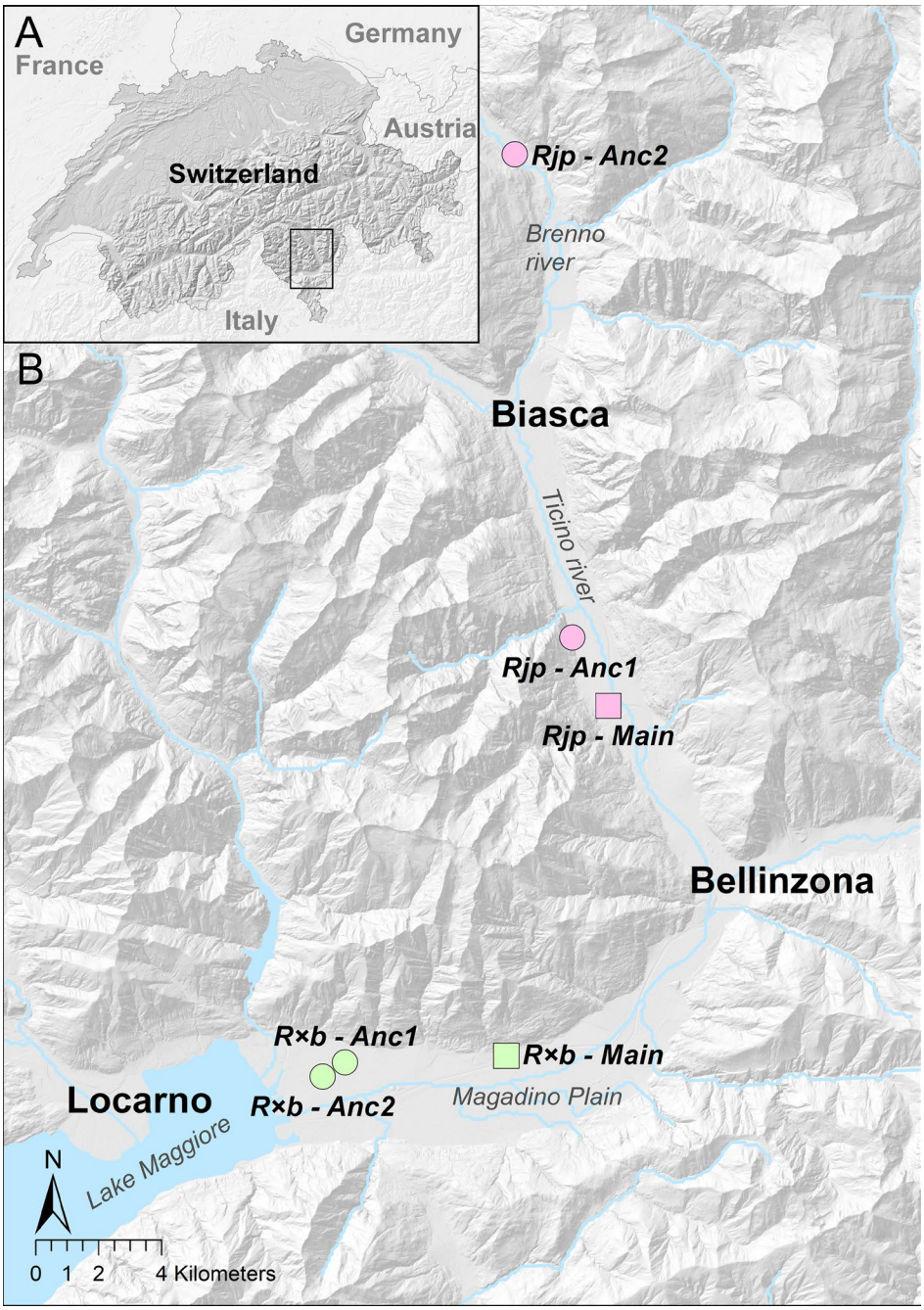

FIGURE 1 | Geographical distribution of the six selected wild populations in Canton Ticino (Switzerland) of *R. japonica* (*Rjp*; light pink points) and *R.* ×*bohemica* (*R*×*b*; light green points). The main sites are represented by squares, while the ancillary sites are represented by circles. (A) Map of Switzerland, and (B) Study area.

The profiles of the obtained trenches and holes were then divided into $40 \times 20\,cm^2$ subunits at both lateral walls (see the coloured parts in blue on the lateral views of Figure 3). All so obtained $40 \times 20\ cm^2$ soil profile subunits in the trenches and in the holes were then dug 10 cm laterally on both sides by removing the soil with a pickaxe, thereby obtaining a final sampling sub-volume of $40 \times 20 \times 10\,cm^3$ each (see the coloured parts in dark brown on the top views of Figure 3). The lateral excavation depth was limited to 10 cm with the aim of linking the registered diameters of the visible underground organs on a soil profile (hereafter referred to as 2D in blue; Figure 3) to a correspondent underground biomass per unit of soil volume (i.e., 3D in dark brown; Figure 3). Ramified organs were considered as two samples only if both cross-sections were visible on the trench soil profiles.

To assess soil compaction, each selected site was tested at the time of excavation with a hand-penetrometer Eijkelkamp (model P1.50/06.01.26), repeating measures at each 5 cm depth at three different points for each soil subunit of 20 cm long and 10 cm large (in the third, sixth and ninth longitudinal portions of each trench, as well as within each subunit designated at the ancillary sites). Obtained soil compaction measurements expressed in kilograms per square centimetre [kg/cm^2] were then averaged for

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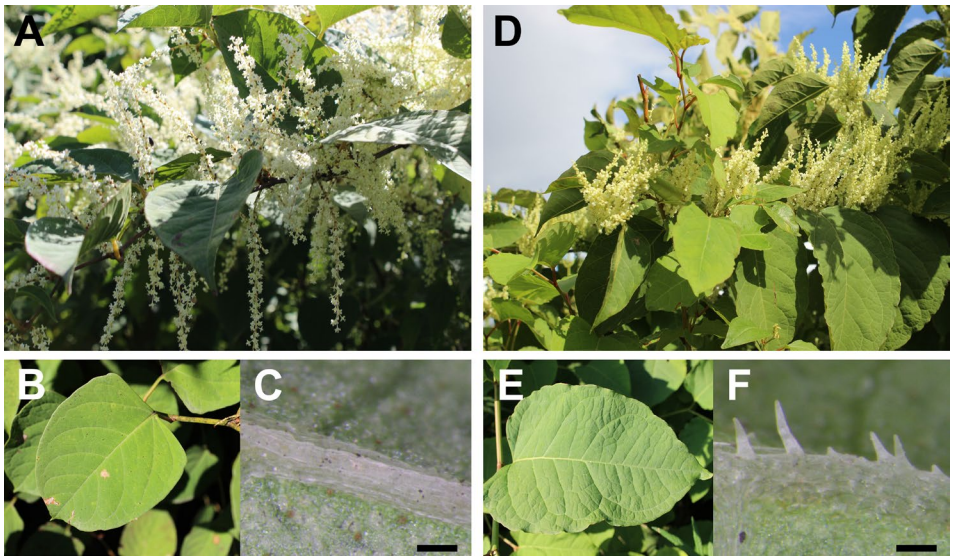

FIGURE 2 | Taxon identification in the six selected wild populations in Canton Ticino (Switzerland). General aspect of flowering plants (A, D), the basic shape of leaves (B, E) and the details of the indumentum on the lower leaf surface (C–F) of *Reynoutria japonica* (*Rjp*) (A–C) and *R.* ×*bohemica* (*R*×*b*) (D–F), respectively. Scale bars: 200 μm.

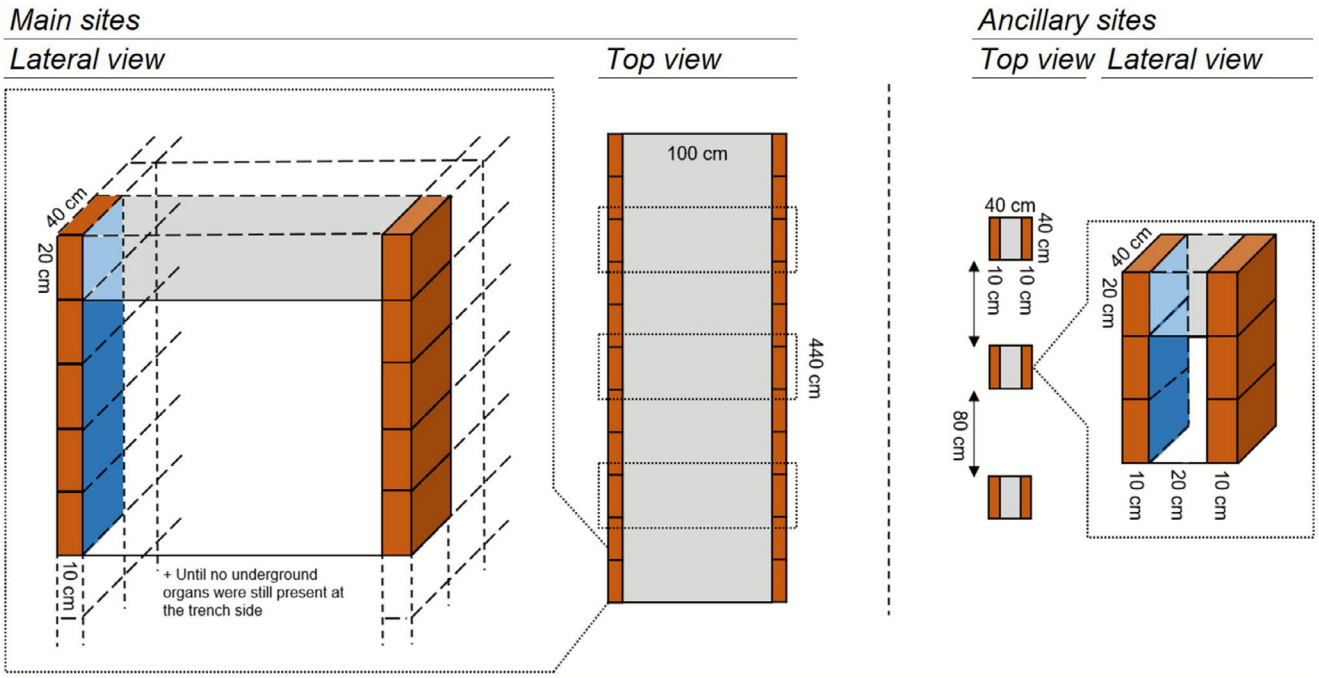

FIGURE 3 | Sampling design. The coloured parts in dark brown and dark blue in the top and lateral views correspond to 3D- and 2D-analyses, respectively. The rhizome segments for the resprouting tests were collected from the top layer represented in light grey (up to 20 cm depth).

each 20-cm layer of soil (i.e., 0–20, 20–40 and 40–60 cm depth). For each soil subunit, the mean of all measurements was computed, excluding values indicative of stone presence (i.e., 50 kg/cm^2) whenever lower compaction values were also recorded within the same soil subunit. The maximum value of 50 kg/cm^2 was retained only when all measurements within a given soil subunit consistently reached this threshold. Soil compaction averages were divided into two categories: low soil compaction ranging from 0 to 25 [kg/cm^2] and high soil compaction ranging from 25 to 50 [kg/cm^2].

2.3 | Measurement of Underground Organs

Underground organs were collected and enclosed in plastic bags separately for each soil subunit and transported to the laboratory facilities at the research campus in Cadenazzo for further processing. Following the removal of residual soil particles by rinsing and subsequent air drying, specimens were differentiated into rhizomes and roots (see Figure 4 for morpho-anatomical description) using the pith-test (Jousson et al. 2024), then measured and parameterised (see Table 1 for details). All underground

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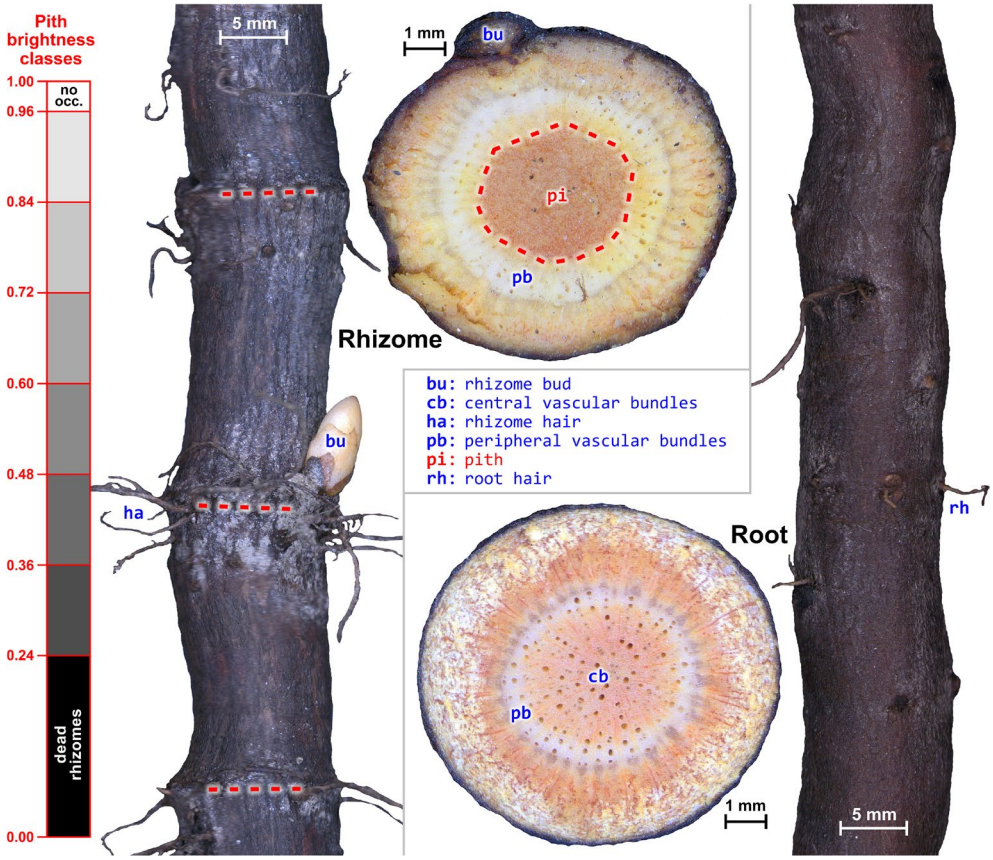

FIGURE 4 | Morpho-anatomical features in rhizomes and roots of the *Reynoutria japonica* complex. While the cross-section of roots consists of vascular bundles only, rhizomes display a central pith tissue (highlighted by the dashed red circle). Its colour and the related resprouting ability can be assessed using the pith brightness classes (greyscale) shown on the left (reproduced from Jousson et al. 2024). Rhizomes also feature nodes bearing a single peripheral dormant bud potentially able to resprout. Abbreviations: bu—rhizome bud; cb—central vascular bundles; ha—rhizome hair; pb—peripheral vascular bundles; pi—pith; rh—root hair.

TABLE 1 | Root and rhizome measurements conducted for each excavated soil subunit.

	Measures on organs	Unit of measure	Precision
3D Soil sample (corresponding to the whole soil subunit volume)	Length	[mm]	1
	Fresh biomass	[g]	10^{-2}
	Number of nodes (rhizomes only)	n	
2D Soil profile (corresponding to the lateral wall of the excavation)	Number of visible cross-sections	n	
	Diameter	[mm]	10^{-2}
	Pith brightness classes (rhizomes only)[a]	Greyscale	

[a]See Jousson et al. (2024) for the details on the pith brightness.

organs were counted. Their diameter was measured with a Toolland digital calliper (precision of 0.01 mm), their length with a ruler (precision of 1 mm) and their fresh weight with a precision balance (Mettler Toledo PB1502-L, precision of 0.01 g). For rhizomes, we additionally counted the number of nodes and assessed the corresponding pith brightness class (1 to 6, from highest to lowest resprouting capacity) as defined by Jousson et al. (2024). Rhizomes exhibiting fully degraded tissues and a darkened central pith—characterised by bright intensity values below 0.24—were excluded from subsequent analyses.

2.4 | Rhizome Resprouting Tests

During the excavations, fresh rhizome samples with a diameter ranging from 0.25 to 3 cm were collected at each site from the top layers (see the coloured parts in light grey in Figure 3). In the laboratory, the collected samples were sectioned into segments measuring 3 ± 0.01 cm in length, ensuring that each contained a node with a dormant bud positioned centrally. The pith brightness was assessed and grouped into three categories according to the resprouting capacity (Jousson et al. 2024): 'Clear' (classes

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1 to 3), 'Intermediate' (classes 4 and 5) and 'Dark' (class 6). For each site, four replicates consisting of 30 segments—10 per pith brightness category—were selected, with care taken to capture the range of diameter variability. The total number of rhizome segments obtained was 720: 360 for *R. japonica* and 360 for *R.* ×*bohemica*. The selected segments were measured for size (i.e., diameter with a precision of 0.01 mm; Toolland digital calliper) and weighed (precision of 0.01 g; Mettler Toledo PB1502-L).

The resprouting experiment was conducted in a greenhouse at the research campus in Cadenazzo. The fresh 3-cm rhizome segments were buried at a depth of 1.5 cm within a 5-cm-deep mixture of sand and loam (soil composition: 1 part silt loam, 1 part sand, 1 part manure and 1 part expanded shale) in plastic trays (Cindy Seed trays with sieve bottom). The experiment spanned a period of 6 months between 15 November 2023 and 15 May 2024. It was run under controlled mean temperature (i.e., 12.5°C ± 5.5°C) and relative air humidity (i.e., 66.5% ± 19.0%) conditions, with soil moisture being maintained daily by adding water. Trays were inspected weekly, and the number of resprouting segments was recorded.

2.5 | Statistical Analysis

We conceived a stepwise approach to build up the needed models and information for answering the three detailed research questions.

Firstly, the distribution of organs was qualitatively illustrated through bar plots (for both 2D and 3D levels). We then calculated—based on the data of our study cases—the effective number of observed nodes under a square metre of ground (n/m^2). The mean number of nodes measured was also reported under conditions of extreme soil compaction, specifically, three layers with high compaction and three with low compaction. In addition, we analysed the distribution patterns of the underground organs in relation to the different putative influential factors (i.e., taxon, soil layer depth and soil compaction) using the fresh biomass (3D analyses) as the response variable across fitting linear mixed models (*lmer* function in LME4 package; Bates et al. 2015) with the sampling site as a random factor. For rhizomes, we additionally ran models using the number of nodes as the response variable.

In a second step, the rhizome resprouting capacity was assessed as a binary response (resprouting vs no resprouting). A binomial model (fitting generalised linear model, binomial multivariate) was performed (*glmer* function in LME4 package; Bates et al. 2015), using the taxon, rhizome diameter and pith brightness categories as explanatory variables and the sampling site as a random factor. Variance inflation factors (*vif*) were computed, and variables exhibiting multicollinearity were excluded from the analysis. A Spearman rank correlation test was performed to assess the relationship between rhizome pith brightness class and rhizome diameter. Resulting resprouting ratios were then visualised by means of boxplots.

We then developed an allometric model linking the number of visible rhizomes along the soil profiles (n/40 × 60 cm^2; 2D) to a correspondent number of nodes under a square metre of ground (n/m^2). The resprouting capacity model was constructed for each taxon retaining the most important morphological rhizome variable (pith brightness). The expected resprouting potential was calculated for both taxa based on the represented percentages of three pith brightness categories considered (i.e., 'Clear'—'Intermediate'—'Dark') and displayed by means of ternary plots (Smith 2017). By combining the number of visible rhizomes on the soil profile and their pith brightness as a proxy for the resprouting capacity, we finally estimated the expected number of resprouting nodes, hereafter referred to as the overall resprouting potential. Expected resprouting node curves were then visualised to support the development of graphic scales applicable in the field and related interpretation.

Statistical tests within boxplots were performed using non-parametric Wilcoxon tests for pairwise comparisons (Hollander and Wolfe 1973) with a false discovery rate correction (Benjamini and Yekutieli 2001). Significant nominal levels of 5% were used for general and pairwise comparisons. For the modelling approaches, estimates, standard deviations, *t* values, confidence intervals (2.5% and 97.5%), *p* values (at the 0.1%, 1% and 5% levels) and *vif* values were calculated for single retained variable. Correlations were calculated using the Spearman method (Spearman 1904). All modelling and statistical analyses were performed in R (RStudio Core Team 2023).

3 | Results

3.1 | Distribution Patterns of Underground Organs

Rhizome biomass was mainly concentrated within the top 40 cm of soil, while roots became more frequent with increasing soil depth and became proportionally dominant starting from 40 to 60 cm depth (3D, Figure 5). The deepest roots were found at the 100–120 cm depth, whereas rhizomes did not penetrate below 60–80 cm depth, where they were present at very low proportions. Concurrently, the number of nodes decreased with both depth and soil compaction (3D, Figure 6). The distribution of the number of organs (in absolute values) along the soil profile is illustrated in Figure S1 (2D).

The distribution of the fresh rhizome biomass in the soil displayed a significant correlation with the soil layer but not with the taxon or soil compaction (Table 2). The distribution of the rhizome nodes was significantly correlated with both the depth of the soil layer and soil compaction. In contrast, none of the considered explanatory variables displayed a significant correlation with the distribution of root fresh biomass.

The mean number of observed nodes per square metre of ground was 2646 ± 221 n/m^2. Under conditions of consistently low soil compaction—defined as three layers registering below 25 kg/cm^2—we observed up to 3825 nodes per square metre. In contrast, when all three layers exhibited compaction levels exceeding 25 kg/cm^2, the number of nodes per square metre dropped to 1825 nodes.

3.2 | Rhizome Resprouting Capacity

Biomass exhibited significant multicollinearity (*vif*) with rhizome diameter and was excluded from the resprouting model. The resprouting capacity of rhizomes significantly depended on

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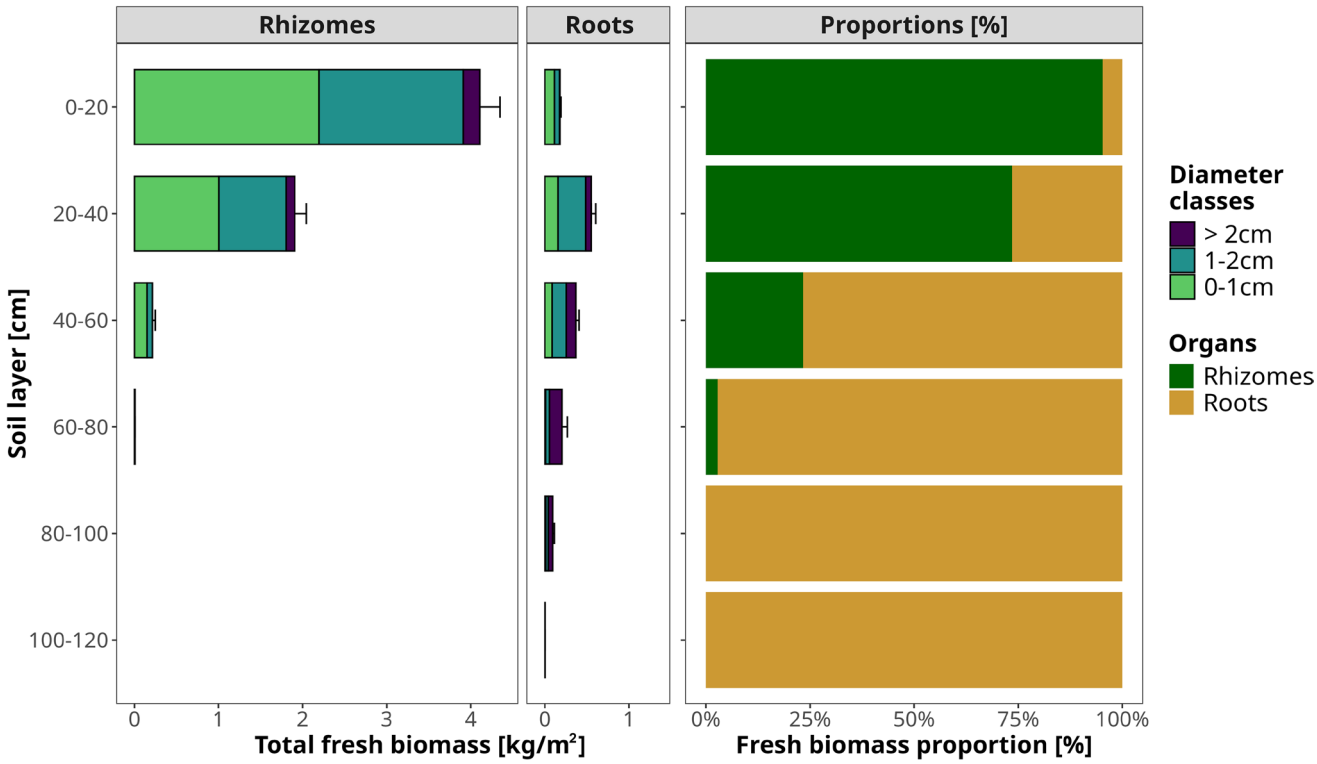

FIGURE 5 | Distribution patterns of rhizomes and roots of *R. japonica* and *R.* ×*bohemica* (six sites). Distribution of the fresh organ biomass in the soil (3D) with standard error bars.

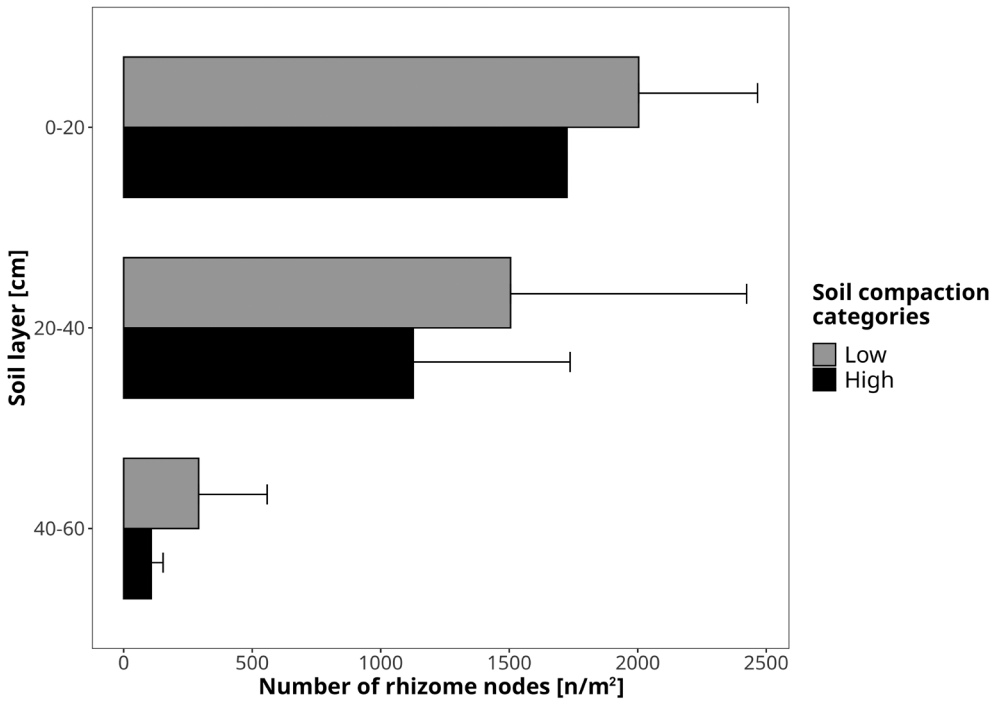

FIGURE 6 | Distribution patterns of rhizomes of *R. japonica* and *R.* ×*bohemica* (six sites). Distribution of the rhizome nodes in the soil (3D) with standard error bars. Soil compaction averages were divided into two categories: low soil compaction ranging from 0 to 25 [kg/cm^2] and high soil compaction ranging from 25 to 50 [kg/cm^2].

pith brightness, rhizome diameter and taxon (Table 3). *R.* ×*bohemica* displayed higher average resprouting ratios (i.e., 69.7%) than *R. japonica* (i.e., 61.4%; see also Figure 7 for details). The Spearman analysis further revealed a significant correlation between rhizome pith brightness class and rhizome diameter (p value < 0.01; see Figure S2).

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TABLE 2 | Estimate statistics of the fitted linear mixed models for rhizome and root distribution patterns (fresh biomass of organs and number of rhizomes nodes; 3D) in *R. japonica* and *R.* ×*bohemica* ($n = 108$ soil samples).

Variable	Estimate	Std. error	*t* value	CI 2.5%	CI 97.5%	*p*	*vif*
Rhizome fresh biomass							
Intercept	240.09	32.81	7.32	180.86	299.20	***	
Taxon	3.07	35.49	0.09	−61.93	67.92		1.00
Soil layer	−61.32	15.32	−4.00	−92.23	−33.29	***	2.13
Soil compaction	−1.27	0.87	−1.45	−2.84	0.47		2.13
Number of rhizome nodes							
Intercept	122.71	22.42	5.57	81.69	163.87	**	
Taxon	−1.77	28.66	−0.06	−55.18	51.54		1.00
Soil layer	−24.53	7.30	−3.36	−40.22	−11.10	**	2.35
Soil compaction	−1.03	0.43	−2.39	−1.82	−0.08	*	2.35
Root fresh biomass							
Intercept	5.38	8.47	0.64	−10.06	20.75		
Taxon	4.08	7.64	0.53	−9.66	17.80		1.00
Soil layer	3.90	4.47	0.87	−4.72	12.10		1.90
Soil compaction	−0.05	0.24	−0.21	−0.48	0.40		1.91

Note: Levels of significance are indicated as follows: ***$p < 0.001$; **$p < 0.01$; *$p < 0.05$.

TABLE 3 | Estimate statistics of the fitted generalised linear mixed model for resprouting capacity of *R. japonica* and *R.* ×*bohemica* ($n = 720$ rhizome segments).

Variable[a]	Estimate	Std. error	*t* value	CI 2.5%	CI 97.5%	*p*	*vif*
Intercept	2.06	0.31	6.72	1.47	2.69	***	
Pith brightness[b]	−0.62	0.07	−9.45	−0.75	−0.50	***	1.36
Diameter	0.10	0.02	4.17	0.06	0.15	***	1.37
Taxon	0.55	0.18	3.04	0.13	0.98	**	1.04

Note: Levels of significance are indicated as follows: ***$p < 0.001$; **$p < 0.01$; *$p < 0.05$.
[a]Weight was removed to avoid multicollinearity with diameter (high *vif* values).
[b]See Jousson et al. (2024) for the details on the pith brightness.

3.3 | Estimating the Overall Resprouting Potential

The resprouting capacity model was predicted for each taxon retaining the most explanatory morphological rhizome variable (i.e., the pith brightness) and the different percentages of each respective pith brightness category: 'Clear'—'Intermediate'—'Dark' (Ternary plots; Figure 8A). Figure 8B reports the significant correlation between the total number of visible rhizome cross-sections along the soil profile (2D) and the corresponding total number of observed nodes under a square metre of ground (coefficient = 140; p value < 0.01). We estimated the number of nodes expected to resprout based on the pith brightness of the related rhizomes. The number of expected resprouting nodes was 1981 n/m^2 for *R. japonica* (SE range: 1783–2179 n/m^2) and 1935 n/m^2 for *R.* ×*bohemica* (SE range: 1630–2240 n/m^2).

To facilitate visual interpretation, the proportions of the three different pith brightness categories were represented using ternary plots, providing a multidimensional proxy for resprouting capacity (Figure 8A). This information was then used to adjust the total number of nodes (Figure 8B) to an expected number of resprouting nodes, illustrated as response curves (Figure 8C).

4 | Discussion

4.1 | Rhizomes Versus Roots

In the extant literature, there is a paucity of attention paid to the differentiation between rhizomes and roots and their importance for eradication efforts (Dommanget et al. 2019; Jousson et al. 2024). It is generally accepted that taxa of the *Reynoutria japonica* complex may extend their underground system to a depth of up to 1.5–2 m (Child and Wade 2000; Smith et al. 2007; Macfarlane 2011; Shaw 2013; Fennell et al. 2018), whereas rhizomes are mainly

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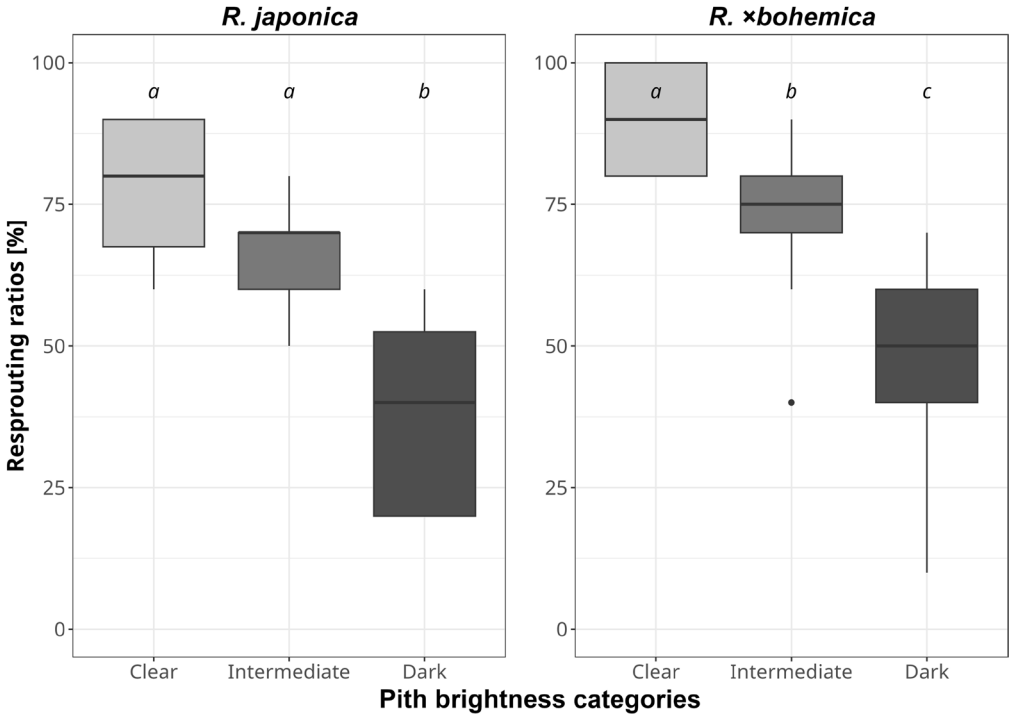

FIGURE 7 | Boxplots of the resprouting ratios (experiment time = six months; $n = 720$) of rhizome segments of *R. japonica* and *R. ×bohemica*, according to taxa and the three pith brightness categories. Different letters represent significant differences (p value < 0.05) according to a pairwise Wilcoxon test using a false discovery rate correction of p value (Benjamini and Yekutieli 2001).

concentrated in the upper 30 cm of the soil profile with only a few extreme cases reaching 1 m in soil depth (Adachi et al. 1996b; Dommanget et al. 2019). Our study confirms that the rhizome biomass is mainly situated in the first 40 cm of soil, whereas root proportions become higher below 40 cm in depth (Figure 5 and Figure S1). Reports suggesting the presence of rhizomes at depths of several metres are likely to be inaccurate, probably resulting from misidentification between rhizomes and roots and/or from the artificial deposition of rhizome-contaminated soil through anthropogenic or natural mechanical processes of soil reworking (Dommanget et al. 2019; Jousson et al. 2024).

Laterally, the Japanese knotweeds extend their rhizomes several metres beyond the outermost aerial shoots, contributing to substantial horizontal spread (Pridham et al. 1966; Smith et al. 2007; Dommanget et al. 2019; Fennell et al. 2018; Martin et al. 2020). Fennell et al. (2018) demonstrated that *Reynoutria japonica* rhizomes are typically confined to a horizontal radius of two meters from above-ground stems in small stands and up to 2.5 m in larger ones, with extensions beyond this range being uncommon. The rhizomes can adapt their growing form to the environmental conditions, which results in thick and short 'phalanx' rhizomes when growing in full light and thin and long 'guerrilla' rhizomes when developing under full shady conditions and/or mechanical stress (Martin et al. 2020). Reported differences in the soil distribution and anatomical features of the two underground organs may be readily explained by their different functions: while rhizomes tend to have a horizontal development and an exploratory function for the expansion of the populations and the subsequent vegetative reproduction through energy storage, roots mostly serve to anchor the plants vertically (Beerling et al. 1994; Adachi et al. 1996b; Dommanget et al. 2019), supporting water and nutrient acquisition as well as carbohydrate storage (Price et al. 2001; Gregory 2007). Furthermore, the penetration ability of rhizomes in the soil (i.e., the number of nodes; Figure 6) significantly depends on soil compaction, whereas the depth of soil penetration by roots seems to be independent of soil compaction (Table 2).

4.2 | Rhizome Ontogeny

Through the present study, we proposed to use the pith colour as a key rhizome characteristic for assessing the capacity of the organ in an undisturbed knotweed population. Our results indicate that the resprouting capacity of the rhizome nodes is significantly linked to the taxon, the organ's diameter and the related pith brightness (Table 3, Figure 7 and Figure S2). The influence of the ontogenetic developmental stage on the resprouting capacity of the rhizomes is confirmed to be revealed by the pith brightness as already reported by Jousson et al. (2024). The general higher resprouting capacity of hybrids with respect to the parent taxa has been already demonstrated by Bímová et al. (2003), Pyšek et al. (2003), Bailey et al. (2009), Zhang et al. (2016) and Kadlecová et al. (2022). Furthermore, the increased node density within the soil correlates with greater establishment success (Francis et al. 2008; Lawson et al. 2021). The length of rhizome and stem fragments also significantly enhances regeneration success due to the amount of stored resources (Sásik and Pavol Jr 2006; Francis et al. 2008), whereas shorter fragments are less viable and more susceptible to burial, making size reduction a potentially effective control strategy (Francis et al. 2008).

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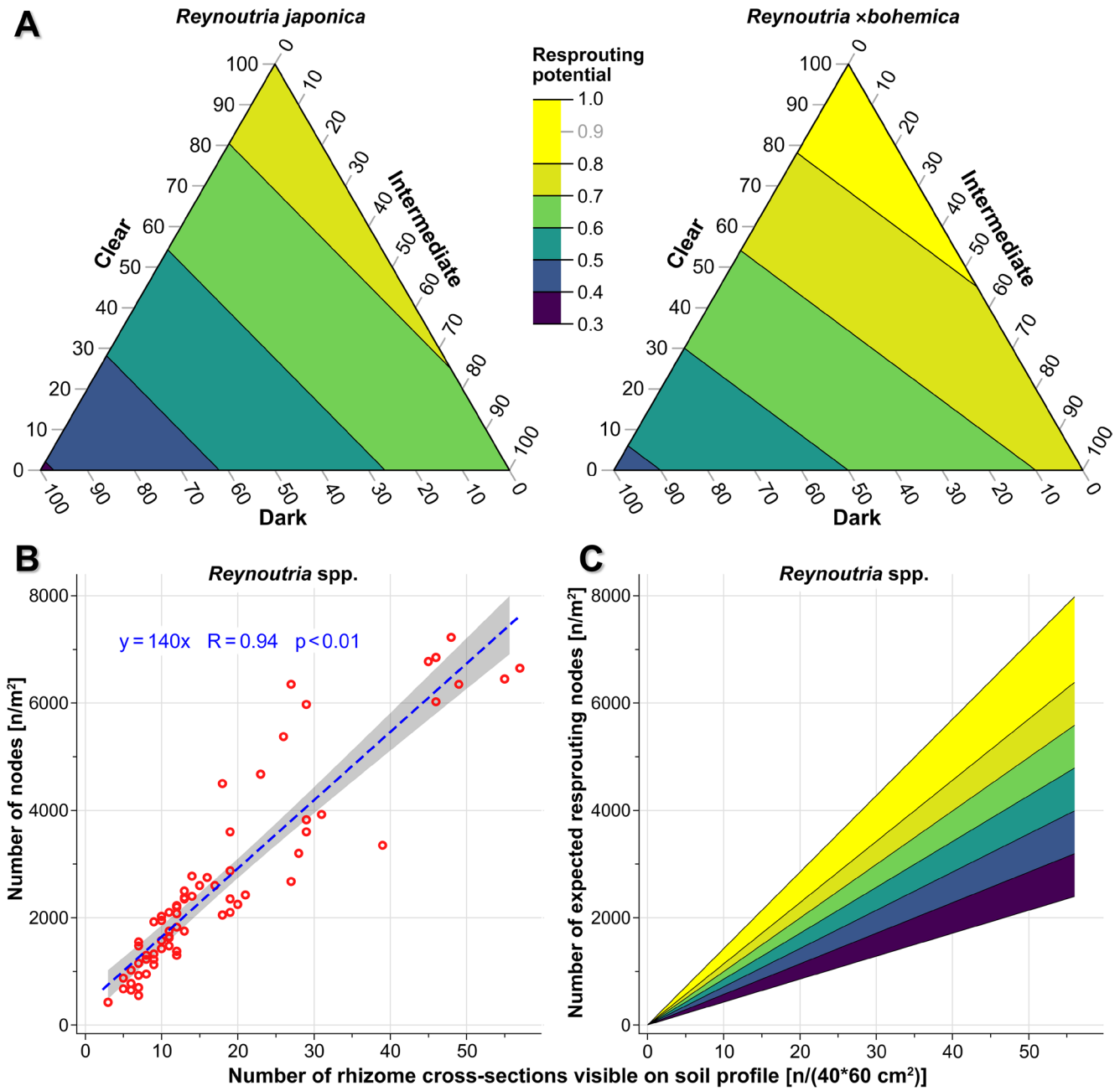

FIGURE 8 | Allometric analyses and modelling of the overall resprouting potential of *R. japonica* and *R. ×bohemica* rhizomes. (A) Ternary plots illustrating the resprouting potential modelled for each taxon separately and for the different percentages of each pith brightness category ('Clear'—'Intermediate'—'Dark'); (B) Total number of observed nodes under a square metre of ground in relation to the total number of visible rhizome cross-sections along the soil profile (2D); (C) Curves illustrating the number of expected resprouting nodes under a square metre of ground based on the number of visible rhizome cross-sections (see B) and the predicted resprouting potential (see A).

4.3 | Overall Resprouting Potential in Knotweeds

The quantification of visible rhizomes along the soil profile enabled estimation of the number of expected resprouting nodes—overall resprouting potential—by integrating their observed abundance with their respective pith brightness, which was used as a proxy for resprouting capacity (Figure 8). Rhizome pith brightness can be easily and directly assessed in the field. These predictions were then presented as resprouting node curves to facilitate the interpretation and the practical implementation in the field. These protocols offer a promising framework for correctly evaluating the regeneration potential and for adapting the control measures in populations of Japanese knotweeds. Further detailed research within treated populations is nevertheless needed to refine the application protocols and to integrate them into the case-dependent most effective eradication strategies.

The capacity of Japanese knotweeds to regenerate from even small rhizome fragments renders them exceptionally challenging to manage (Bímová et al. 2003; Pyšek et al. 2003; Lawson et al. 2021). Jones et al. (2018) underscore the importance of

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aligning treatment strategies with the phenological and physiological dynamics of Japanese knotweeds, showing that approaches maximising herbicide coverage and targeting rhizome source–sink relationships yield the most effective long-term control. Moreover, combining mechanical control with the restoration of competitive native species has proven to be an effective management strategy for limiting the vigour and spread of Japanese knotweeds (Dommanget et al. 2015). On the contrary, inadequate assessment of their resprouting potential may result in ineffective control strategies and economically burdensome reinvasions (Richards et al. 2012; Zhang et al. 2016; Martin et al. 2020). Understanding, anticipating and forecasting the resprouting capacity of Japanese knotweeds is an important prerequisite for determining the control or eradication efforts required for these highly invasive plant species (Lowe et al. 2000; Künzi et al. 2015; Lavoie 2017).

5 | Conclusion

Combining the distribution of underground organs with the proposed approach to assess the overall rhizome potential provides a substantial foundation for planning targeted and cost-effective control measures. Japanese knotweeds exhibit robust clonal dispersal driven by their resprouting rhizomes, a trait that underpins their pronounced invasive potential. In the context of management strategies, it is thus imperative to differentiate between rhizomes and roots. In instances where the knotweed populations have remained unaffected by substantial anthropogenic disturbances or soil alterations and movements, the rhizomes, which constitute the problematic organs that can resprout, are concentrated in the first 40 (−60) cm of soil. At depths greater than 60 cm, rhizomes were nearly absent, with only roots being observed. This study provides an initial framework that may support management optimisation and assist in selecting the most appropriate control measures as part of an informed intervention strategy.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **FIGURE S1:** Distribution patterns of rhizomes and roots of *R. japonica* and *R. ×bohemica* (six sites). Distribution of the number of visible organs' cross-sections along the soil profile (2D) with standard error bars. **FIGURE S2:** Rhizome diameter in relation to the pith brightness classes for *R. japonica* and *R. ×bohemica* (resprouting ratios tests, experiment time = six months; $n = 720$).

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