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Comparing field-based management approaches for invasive Winter Heliotrope (*Petasites pyrenaicus*, Asteraceae)

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Abstract

Winter Heliotrope (*Petasites pyrenaicus*, previously *P. fragrans*), is a persistent, rhizome-forming species found throughout the Mediterranean region and North Africa and is an Invasive Alien Plant (IAP) in the UK and Ireland. *P. pyrenaicus* excludes native flora by forming a dense, compact canopy that persists for much of the growing season, and is often found growing in rough ground, riparian areas and along communication routes, incurring significant management costs at sites of conservation interest. Our study describes the first field-based assessment of *P. pyrenaicus* control treatments, testing 12 physical and/or chemical treatments in replicated 1 m^2 plots over four years and one chemical treatment over three years. Treatments focused on understanding phenology and resource allocation to exploit rhizome source-sink relationships in *P. pyrenaicus*. Multiple-stage glyphosate- and picloram-based treatments reduced leaf canopy cover to zero (%) over time, though no treatment completely eradicated *P. pyrenaicus*. When designing management strategies, effective *P. pyrenaicus* control may be achieved by a single annual soil and/or foliar application of picloram at 1.34 kg AE ha^{-1} in spring, or by a single annual foliar application of glyphosate in spring at 2.16 kg AE ha^{-1}. Control is not improved by the addition of other herbicides or physical treatment methods, underlining the importance of these herbicides for perennial invasive plant management. This work confirms the importance of considering plant phenology, resource allocation and rhizome source-sink relationships, to increase treatment efficacy and reduce the environmental impacts associated with the management of *P. pyrenaicus* and other invasive, rhizome forming species.

Keywords

field trial, herbicide, Integrated Weed Management (IWM) system, invasive alien plants (IAPs), invasive non-native species (INNS), *Petasites fragrans*, *Petasites pyrenaicus*, rhizome source-sink, Winter Heliotrope

Introduction

Winter Heliotrope (*Petasites pyrenaicus* (L.) G. López, previously known as *P. fragrans* (Vill.) C. Presl): Asteraceae) is a persistent dioecious, rhizomatous, herbaceous perennial native to the Mediterranean region and North Africa (Desjardins et al. 2016; Stace 2019). The non-native range of *P. pyrenaicus* includes Europe, New Zealand, Australia and the northwest coast of the United States; in the British Isles (United Kingdom (UK) and Ireland) it is one of several *Petasites* spp. considered as invasive alien plants (IAPs) (National Roads Authority 2010; GB Non-Native Species Secretariat 2011a, b, c; Global Biodiversity Information Facility 2020). It was introduced as an ornamental plant to the UK in 1806, first recorded as naturalised by 1835 (Clement and Foster 1994; GB Non-Native Species Secretariat 2011a; Stace 2019), and its range continues to expand throughout the UK (except in northern England and Scotland) and Ireland, typically associated with rough ground, riparian areas and communication routes (Clement and Foster 1994; National Roads Authority 2010; GB Non-Native Species Secretariat 2011a; Desjardins et al. 2016; Stace 2019). *P. pyrenaicus* primary mode of spread in its non-native range is clonally through asexual dispersal, i.e. rhizome expansion and fragmentation. Anthropogenic and natural disturbance has been reported to increase dispersal (GB Non-Native Species Secretariat 2011a; Cornwall LNR's 2013). Desjardins et al. (2016) reported hybridisation of *P. japonicus* (Giant butterbur) with *P. pyrenaicus* in southern England (UK), the hybrid offspring of which (*P. japonicus* × *P. pyrenaicus*) were highly fertile.

P. pyrenaicus excludes native flora by light exclusion from a low growing, compact leaf canopy (Fig 1.). Beneath the canopy, a persistent mulch of dead leaves suppresses native plant species germination (GB Non-Native Species Secretariat 2011a; Booy et al. 2015). Belowground *P. pyrenaicus* rhizome growth is largely within the first 50 cm of the soil profile (Fig. 1) but varies depending upon establishment of the patch and local ground conditions (Jones 2015). Rhizomes grow laterally at 0.5–1.0 m yr^{-1} (Hoare 2014), with new ramets spreading aboveground growth and adventitious roots (Jones 2015) leading to growth of dense monospecific patches. In riparian habitats, the relatively low soil binding capabilities of *P. pyrenaicus* rhizomes and adventitious roots leads to increased bank erosion (Fig. 1; Jones 2015).

Long-term, field relevant research to underpin the management of many IAPs is lacking (Kettenring and Adams 2011). Specifically, in the UK there is limited guidance available for the control of *P. pyrenaicus* and other introduced *Petasites* spp. including *P. japonicus* (Giant butterbur) and *P. albus* (White butterbur), which incur significant management costs at sites of conservation importance and along roadsides (Parrott 2008; National Roads Authority 2010; Stace 2019; GB Non-Native Species Secretariat 2011a, b, c). Management practices for rhizome-forming species must account for the linkage between above and belowground tissues to inform the correct timing, concentration and intensity of control treatment application (Jones et al. 2018). Extensive above and belowground biomass may hamper efforts to deplete rhizome reserves and strong seasonal changes in *P. pyrenaicus* rhizome source-sink strength affects herbicide translocation to belowground tissues (Jones 2015).

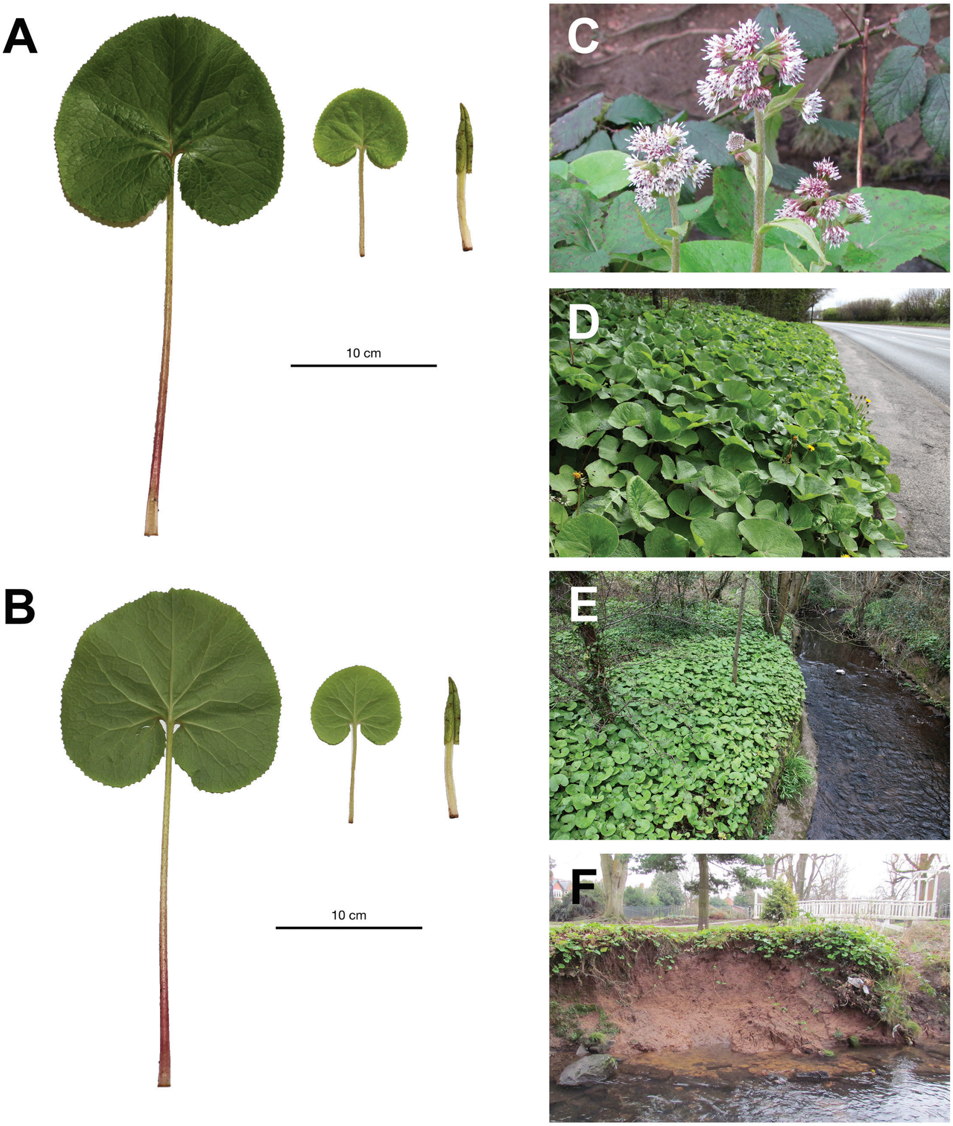
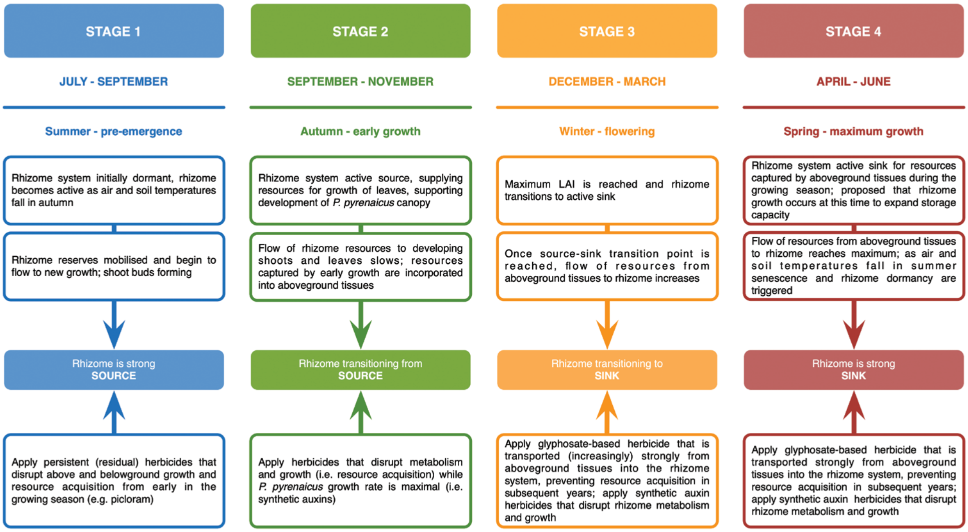


Figure 1. *P. pyrenaicus* - Winter Heliotrope. Where **A** adaxial and **B** abaxial leaf surfaces (immature leaf and leaf bud is also shown). Leaves are suborbicular and not lobed; up to 20 cm across, petioles to 30 cm **C** inflorescence (November-February). Erect flowering stems (to 30 cm) bear few medium-broad bracts and a panicle of capitula; flowers are white tinged purple and strongly almond-scented **D** and **E** low growing, compact, closed canopy of leaves growing adjacent to a road (**D**) and stream (**E**) **F** *P. pyrenaicus* growing on the bank of Roath Brook (Cardiff, UK). Note depth of rhizome system (bank is ~2 m above the river channel), that the majority of rhizome is concentrated in the top 50 cm of the soil profile and erosion of the riverbank due to ineffective binding of soil by *P. pyrenaicus* rhizomes and roots. (Images courtesy of D. Jones)

To our knowledge, only one source of information for the control and management of *P. pyrenaicus* exists, which is not based on empirical data (National Roads Authority 2010). The use of glyphosate, an aromatic amino acid (AAA) synthesis inhibitor, and metsulfuron-methyl, an acetolactate synthase (ALS) inhibitor is advised for roadside management. Alternatively, complete physical excavation of above and belowground (rhizome) biomass and integration of physical with chemical treatments is also recommended (National Roads Authority 2010). Methods involving cutting roadside vegetation will increase the dispersal of vegetative *P. pyrenaicus* propagules, similar to other rhizome-forming species, e.g. Japanese Knotweed (*Reynoutria japonica*; Bashtanova et al. 2009; Jones et al. 2020).

The primary objective of this study was to employ an evidence-based experimental approach to provide a robust, appropriately scaled field evaluation of *P. pyrenaicus* management strategies. The Integrated Weed Management system approach tested three treatment response categories: physical (e.g. covering), chemical (e.g. application of herbicide) and integrated (e.g. digging before herbicide spraying). Our study linked *P. pyrenaicus* physiology (i.e. resource allocation and rhizome source-sink strength) with physical or chemical control method target (i.e. resource depletion, uptake, movement and metabolism) within a four-stage mechanistic model (Fig. 2). This approach to treatment efficacy evaluation was similar to that successfully employed in Japanese Knotweed (*R. japonica*) control (Jones et al. 2018). Briefly, Stage 1; summer disruption of new *P. pyrenaicus* aboveground growth and depletion of rhizome reserves (note that this stage was not tested specifically in the current experiment). Stage 2, autumn treatment against metabolism and growth, reducing resource acquisition. Stage 3, winter treatment at maximum leaf expansion, targeting the transition point where the rhizome becomes a reserve. Stage 4, spring coupling of aboveground resource translocation to the rhizome with herbicide application, maximising translocation to belowground tissues.



STAGE 1	STAGE 2	STAGE 3	STAGE 4
JULY - SEPTEMBER	SEPTEMBER - NOVEMBER	DECEMBER - MARCH	APRIL - JUNE
Summer - pre-emergence	Autumn - early growth	Winter - flowering	Spring - maximum growth
Rhizome system initially dormant, rhizome becomes active as air and soil temperatures fall in autumn	Rhizome system active source, supplying resources for growth of leaves, supporting development of *P. pyrenaicus* canopy	Maximum LAI is reached and rhizome transitions to active sink	Rhizome system active sink for resources captured by aboveground tissues during the growing season; proposed that rhizome growth occurs at this time to expand storage capacity
Rhizome reserves mobilised and begin to flow to new growth; shoot buds forming	Flow of rhizome resources to developing shoots and leaves slows; resources captured by early growth are incorporated into aboveground tissues	Once source-sink transition point is reached, flow of resources from aboveground tissues to rhizome increases	Flow of resources from aboveground tissues to rhizome reaches maximum; as air and soil temperatures fall in summer senescence and rhizome dormancy are triggered
Rhizome is strong SOURCE	Rhizome transitioning from SOURCE	Rhizome transitioning to SINK	Rhizome is strong SINK
Apply persistent (residual) herbicides that disrupt above and belowground growth and resource acquisition from early in the growing season (e.g. picloram)	Apply herbicides that disrupt metabolism and growth (i.e. resource acquisition) while *P. pyrenaicus* growth rate is maximal (i.e. synthetic auxins)	Apply glyphosate-based herbicide that is transported (increasingly) strongly from aboveground tissues into the rhizome system, preventing resource acquisition in subsequent years; apply synthetic auxin herbicides that disrupt rhizome metabolism and growth	Apply glyphosate-based herbicide that is transported strongly from aboveground tissues into the rhizome system, preventing resource acquisition in subsequent years; apply synthetic auxin herbicides that disrupt rhizome metabolism and growth

Figure 2. Conceptual four stage mechanistic model of phenological changes in *P. pyrenaicus* growth, resource allocation and rhizome source-sink strength during the temperate northern hemisphere growing season (adapted from Jones et al. 2018). LAI = leaf area index. Note linkage of above and belowground growth processes with changes in source-sink strength and that rhizome tissue sink strength increases through the winter from November, reaching a peak in April-June during senescence.

Here we report on the first, multi-year evaluation of 13 control strategies for *P. pyrenaicus*, following an Integrated Weed Management system approach. In particular, we considered whether targeting the rhizome source-sink switch can provide more effective and sustainable *P. pyrenaicus* control, by reducing pesticide application to minimise ecological impact.

Methods

Field trial site selection

The four-year experiment was conducted at a single site in south Wales (UK; Fig. 3) and the geological and hydrological conditions of the site are provided in Suppl. material 1. *P. pyrenaicus* was extensive and well established at the site, being present *in-situ* for more than 20 years. For the present study, control methods were applied from 2013 to 2017.

Experimental design

Thirty 1 m^2 treatment and control plots were established (Suppl. material 2), with each plot surrounded by a 10 cm buffer zone. Physical, chemical and/or integrated treat-

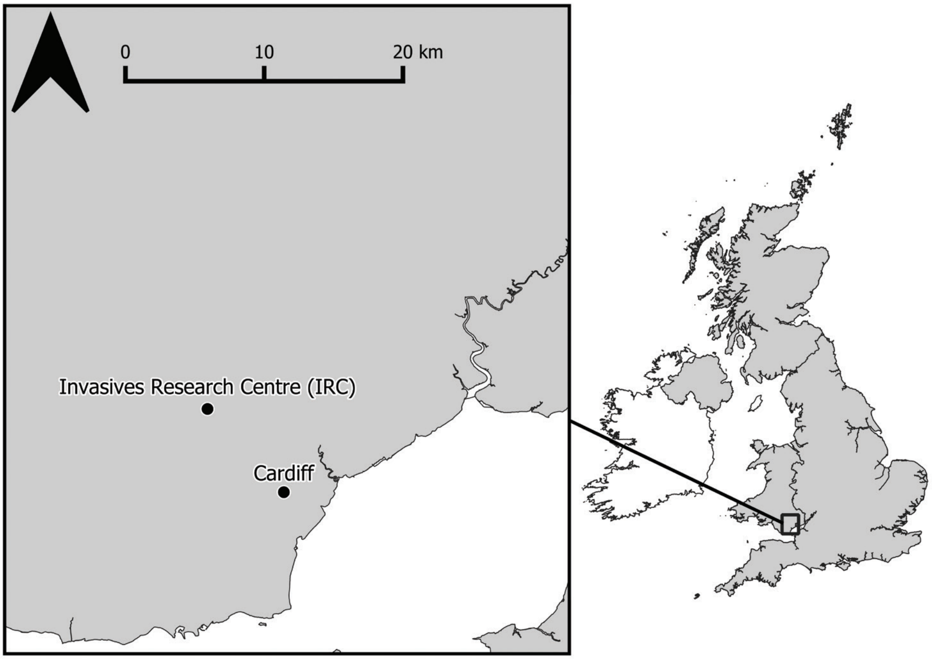


Figure 3. Map of the study area. Inset shows location of Invasives Research Centre (IRC) in south Wales, UK (WGS 84: 51.534124, -3.259120).

ments were applied to the whole of each treatment plot. Each treatment group was replicated twice with the exceptions of the untreated control plot and covering treatment (Covering, N/A, Win.; Table 1) which were replicated once, and one glyphosate-based herbicide treatment replicated four times (Gly., 2.16, Fol., Spr.; Table 1). No dummy treatments were applied to the untreated plots as the application of dilute quantities of herbicide from the spraying equipment may have influenced untreated plot responses. Treatment assignment was randomised, with the exception of the picloram treatment group (Pic., 1.34, Soil+Fol., Spr.; Table 1) which could not be legally sited near watercourses (Suppl. material 3).

In the first year of treatment (2013), plot assessment was undertaken on 01 May prior to treatment application, and again on 21 August following treatment application. In subsequent years, assessment was undertaken while the plant was in full growth (between 16 April and 01 July), with the final assessment made following application of all treatments on the 01 September 2017, while the plant was in full growth and prior to senescence. Aboveground *P. pyrenaicus* leaf canopy percentage cover (%) was recorded from each plot as the response variable.

Table 1. Physiochemical Winter Heliotrope treatments, showing treatment group abbreviation, concentration of herbicide active ingredient (a.i.) within each product tested (g L^{-1}), application rate measured in kilogrammes acid equivalent per hectare (kg AE ha^{-1}), application method (e.g. foliar spray) and seasonal timing. Underlined herbicide active ingredients indicate product mix; italicised processes represent physical components of integrated physiochemical control treatments; Roman numerals represent multi-seasonal application of physiochemical control treatments. Specific timing of seasonal application: autumn (stage 2) = September-November; winter (stage 3) = December-March; spring (stage 4) = April-June. Treatment group abbreviations are provided in the format: treatment, application rate, application method, season of application. Abbreviations used in the treatment groups are as follows: 2,4-D = 2,4-D amine; Ami. = aminopyralid; Clo. = clopyralid; Flu. = fluroxypyr; Gly. = glyphosate; Pic. = picloram; Tri. = triclopyr; Fol. = foliar application; Exc. = excavation; Spr. = spring; Aut. = autumn.

Treatment group abbreviation	a.i. (g L^{-1})	Application rate (kg AE ha^{-1})	Application method	Application timing
Gly., 3.60, Fol., Spr.	Glyphosate (360)	3.60	Foliar spray	Spring
Gly., 2.16, Fol., Spr.	Glyphosate (360)	2.16	Foliar spray	Spring
Gly., 3.60, Fol., Aut.	Glyphosate (360)	3.60	Foliar spray	Autumn
Gly., 2.16, Fol., Spr.+Aut.	Glyphosate (360)	2.16	Foliar spray	i) Spring ii) Autumn
2,4-D, 4.50, Fol., Spr.	2,4-D amine (500)	4.50	Foliar spray	Spring
2,4-D, 4.50, Fol., Aut.	2,4-D amine (500)	4.50	Foliar spray	Autumn
Ami.+Flu., 0.06+0.20, Fol., Spr.	Aminopyralid (30) & Fluroxypyr (100)	0.06 & 0.20	Foliar spray	Spring
2,4-D+Dic., 1.20+0.42, Fol., Spr.	2,4-D amine (344) & Dicamba (120)	1.20 & 0.42	Foliar spray	Spring
Tri.+Clo., 0.05+0.48, Fol., Spr.	Triclopyr (240) & Clopyralid (60)	0.29 & 0.05	Foliar spray	Spring
Pic., 1.34, Soil+Fol., Spr.	Picloram (240)	1.34	Soil and foliar spray	Spring
Ami.+Tri., 0.05+0.48, Fol., Spr.	Aminopyralid (12) & Triclopyr (100)	0.05 & 0.48	Foliar spray	Spring
Exc.+Gly., N/A+3.60, Fol., Win.+Spr.	Excavation Glyphosate (360)	3.60	Foliar spray	i) Winter ii) Spring
Covering, N/A, Win.	Covering	N/A	Cardboard	Winter

Herbicide product selection and control treatment timing

Herbicide product selection and application timing of the 13 treatments (Table 1) was informed by the consideration of established *P. pyrenaicus* source-sink relationships, and methods used against other rhizome-forming species (Jones et al. 2018; Fig. 2). Full herbicide and spray adjuvant information, including physical properties, areas of use, legal designations, UK inclusion date and manufacturers, is supplied in Suppl. material 3.

Details of treatment groups

Herbicide control treatments – Soil and foliar spray application

Herbicide product(s) were applied at a fixed rate of active ingredient(s) per unit area (L or kg AE ha^{-1}) using a Cooper Pegler CP3 (20 L) Classic knapsack sprayer, fitted with a Cooper Pegler blue flat fan nozzle (AN 1.8). All herbicide products were applied with dye, adjuvant (Topfilm; 1.2 L ha^{-1}) and water conditioner (EasiMix; 1.2 L ha^{-1}) to ensure even coverage and maximise herbicide active ingredient absorption. Herbicide products containing aminopyralid (synthetic auxin) were applied with antifoaming agent (Foam Fighter). All herbicides were foliar applied, except for picloram, which was also applied to any bare ground within the field trial plot due to the persistent soil activity of this herbicide. Following application of all herbicides at the specified application rate (kg AE ha^{-1}; Table 1) the knapsack sprayer was cleaned with 10 L clean water. Following application of herbicide products containing 2,4-D, this was supplemented with 50 ml ammonia-based cleaning fluid (Extra Clear). Weather forecast information (UK Met Office weather app) was consulted prior to treatment application to ensure that no rain was forecast for a minimum of 8 hours post-application. Note that spring aminopyralid and triclopyr foliar spray (TG g1) treatment was tested for 3 years only as this product combination of herbicide active ingredients was newly introduced to market one year after field trial establishment.

Integrated physiochemical control treatment – Excavation

Excavation of the full 1 m^2 field trial plot, to a depth of 0.5 m, was undertaken with a hand shovel in winter (stage 3), breaking up the rhizome system; excavated soil containing rhizome was left *in-situ*. The following spring (stage 4), glyphosate was applied as a foliar spray, at full rate (FR, 3.6 kg AE ha^{-1}), following regrowth of the *P. pyrenaicus* canopy. Excavation and glyphosate foliar spray were repeated in each subsequent winter and spring, respectively.

Physical control treatment – Covering combined with hand pulling

Prior to covering in spring (stage 4), the full 1 m^2 field trial plot was excavated using a hand shovel in winter (stage 3) to a depth of 0.5 m, breaking up the rhizome system;

excavated soil containing rhizome was left in-situ. The treatment area was fully covered for the duration of the experiment, by laying five layers of thick (4.0 mm) cardboard annually over the treatment area and weighted to remain in position (new layers of cardboard being laid over the top of old layers). Visible *P. pyrenaicus* growth emerging around the covering was then hand pulled and left *in-situ* underneath the covering and/or additional covering added to prevent further growth. Covering was the only physical control treatment trialled, as other physical control treatments (pulling, digging and burning) were considered too costly, labour intensive and increased the risk of *P. pyrenaicus* spread.

Data analysis

Following the recommendation of Warton and Hui (2011) for dealing with % data, we applied a logit transformation to the *P. pyrenaicus* leaf canopy percentage cover (%; 1 m^2) data by first converting the % coverage in each field trial plot to proportion coverage (PC), with the addition of the smallest recorded coverage value (0.5%) to both numerator and denominator, to avoid problems with log transformation of the 0% coverage values. This gives an untransformed response variable $PC = (\% \text{ cover} + 0.5)/100.5$, to which the logit transformation is then applied: $y = \log_e(PC/[1-PC])$. The logit transformed data was analysed using a linear model (ANCOVA) considering the interaction between days after treatment (DAT) and treatment group (TG).

We focussed on the change in logit transformed *P. pyrenaicus* cover over time within each individual treatment group, rather than directly comparing slopes across treatments or the untreated control group. This is appropriate to maintain statistical power, given the independence of plots in the sampling design and the relatively low levels of replication within treatment groups. Model residuals were checked and did not violate the assumption of normality (Shapiro test, W = 0.99, p = 0.31).

All data were analysed using R v3.6.3 (The R Development Core Team 2020). The 'emmeans' package (Lenth 2020) was used to determine 95% confidence intervals for each Treatment Group's slope estimates and the 'ggplot2' package (Wickham 2016) was used to generate plots.

Results

Three treatments provided greatest control of aboveground *P. pyrenaicus* growth, defined by reduced leaf canopy cover (Table 2; Fig. 4): spring glyphosate full rate (FR) foliar spray (Gly., 3.60, Fol., Spr.; Table 1), spring glyphosate half rate (HR) foliar spray (Gly., 2.16, Fol., Spr.; Table 1) and spring picloram FR soil and foliar spray (Pic., 1.34, Soil+Fol., Spr.; Table 1). Neither the untreated control group, nor any of the other treatment groups, showed any significant change in *P. pyrenaicus* cover over time (Table 2; Fig. 4).

Application of the synthetic auxins 2,4-D amine (2,4-D, 4.50, Fol., Spr.; 2,4-D, 4.50, Fol., Aut.; Table 1), aminopyralid and fluroxypyr (Ami.+Flu., 0.06+0.20, Fol.,

Table 2. Linear model parameter estimates for changes in Logit transformed Winter Heliotrope canopy cover (%, m^2) as a function of time (days) after treatment started (Fig. 4). Full model statistics: $F_{27,134} = 5.5$, $p < 0.001$, $R^2 = 0.53$. Slope estimates in bold differ significantly from 0 at the a = 0.05 level. Treatment group abbreviations are provided in the format: treatment, application rate, application method, season of application. Abbreviations used in the treatment groups are as follows: 2,4-D = 2,4-D amine; Ami. = aminopyralid; Clo. = clopyralid; Flu. = fluroxypyr; Gly. = glyphosate; Pic. = picloram; Tri. = triclopyr; Fol. = foliar application; Exc. = excavation; Spr. = spring; Aut. = autumn.

Treatment group abbreviation	Intercept ± S.E.	Slope ± S.E.	Slope 95% CI
Untreated control	1.92 ± 1.16	-0.0003 ± 0.0013	-0.0029, 0.0023
Gly., 3.60, Fol., Spr.	-2.39 ± 0.83	**-0.0021 ± 0.0010**	**-0.0040, -0.0002**
Gly., 2.16, Fol., Spr.	-2.71 ± 0.58	**-0.0013 ± 0.0007**	**-0.0027, -0.000003**
Gly., 3.60, Fol., Aut.	-1.43 ± 0.77	-0.0008 ± 0.0009	-0.0027, 0.0012
Gly., 2.16, Fol., Spr.+Aut.	-0.90 ± 0.77	0.0003 ± 0.0010	-0.0016, 0.0022
2,4-D, 4.50, Fol., Spr.	-1.90 ± 0.83	0.0013 ± 0.0010	-0.0006, 0.0032
2,4-D, 4.50, Fol., Aut.	-0.91 ± 0.77	0.0006 ± 0.0009	-0.0012, 0.0025
Ami.+Flu., 0.06+0.20, Fol., Spr.	-1.18 ± 0.83	0.0001 ± 0.0010	-0.0018, 0.0020
2,4-D+Dic., 1.20+0.42, Fol., Spr.	-1.75 ± 0.83	0.0016 ± 0.0010	-0.0003, 0.0035
Tri.+Clo., 0.05+0.48, Fol., Spr.	-1.30 ± 0.82	0.0003 ± 0.0009	-0.0016, 0.0025
Pic., 1.34, Soil+Fol., Spr.	-3.07 ± 0.83	**-0.0020 ± 0.0010**	**-0.0039, -0.00002**
Ami.+Tri., 0.05+0.48, Fol., Spr.	1.96 ± 1.05	-0.0003 ± 0.0015	-0.0033, 0.0027
Exc.+Gly., N/A+3.60, Fol., Win.+Spr.	-0.63 ± 0.82	-0.0003 ± 0.0009	-0.0022, 0.0015
Covering, N/A, Win.	1.28 ± 1.17	-0.0013 ± 0.0014	-0.0040, 0.0015

Spr.), 2,4-D amine and dicamba (2,4-D+Dic., 1.20+0.42, Fol., Spr.), triclopyr and clopyralid (Tri.+Clo., 0.05+0.48, Fol., Spr.), aminopyralid and triclopyr (Ami.+Tri., 0.05+0.48, Fol., Spr.) did not reduce *P. pyrenaicus* canopy cover in the long-term, regardless of application timing (stages 2 and 4, Fig. 4). In contrast, picloram (Pic., 1.34, Soil+Fol., Spr.) significantly reduced *P. pyrenaicus* canopy cover throughout this four-year study, despite picloram only being applied for two years between 2013 and 2015 (picloram was withdrawn from European Union (EU) use 30 June 2015). This treatment rapidly led to 0% cover in both replicates by autumn 2013, with the only brief reappearance being 1% cover in one replicate in spring 2014, which then returned to 0% cover for the remainder of the trial following subsequent treatment application.

Discussion

This study forms the first assessment of *P. pyrenaicus* control treatments, specifically targeting the rhizome source-sink switch (Fig. 2) and utilising an Integrated Weed Management system experimental design. Field-relevant experimental designs are fundamental to inform the control of long-lived perennial, rhizome-forming invasive species. Our approach was designed to account for long-term control response in 12 treatment groups across 28 treatment plots (1 m^2) over four years; spring aminopyralid and triclopyr foliar spray (Ami.+Tri., 0.05+0.48, Fol., Spr.; Table 1) treatment was assessed in two treatment plots over three years following initial treatment application.

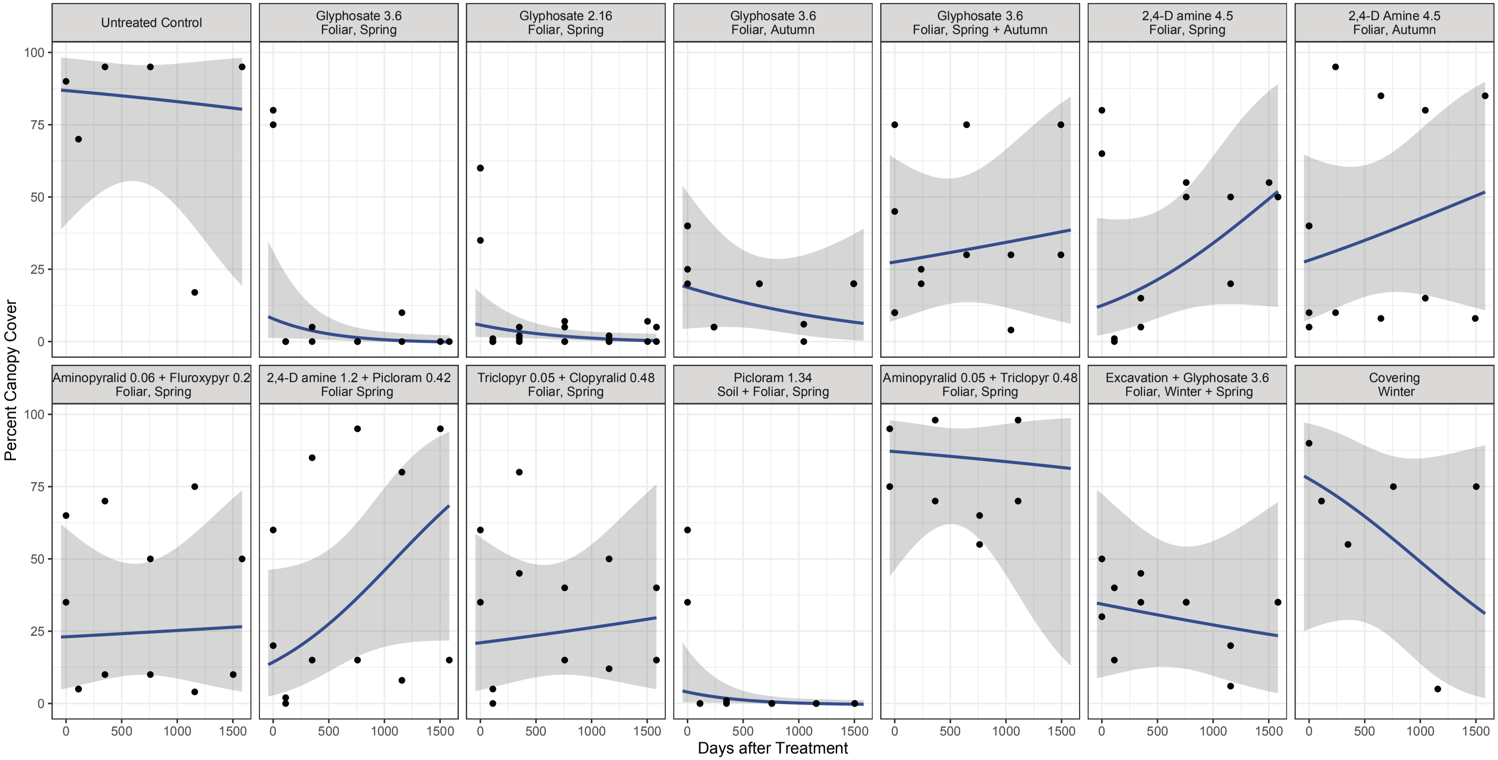


Figure 4. Efficacy of different *P. pyrenaicus* control methods over time, including one untreated control group. Active ingredients, application rates, method and timing are given above each plot. Solid lines and shaded areas (95% CIs) are back-transformed from leaf canopy cover data that was logit transformed (+0.5% in all cases) before fitting a linear model with Days After Treatment and Treatment Group as (interacting) predictor variables ($F_{27,134} = 5.5$, $p < 0.001$, $R^2 = 0.53$).

Physical, chemical and integrated control treatment application was combined with our biological understanding of *P. pyrenaicus*. Autumn (stage 2, Fig. 2) treatments were targeted at metabolism and growth to limit belowground resource acquisition. Winter (stage 3, Fig. 2) treatments tested were intended either to increase efficacy of subsequent herbicide treatment (stage 4, Fig. 2) through disruption (excavation; Exc+Gly., N/A+3.60, Fol., Win.+Spr.; Table 1) of belowground tissues, or deplete rhizome resources through resource restriction (light, covering; Covering, N/A, Win.; Table 1) throughout the growing season. Herbicide-based control methods applied in spring (stage 4, Fig. 2) were either coupled to mass flow of photosynthates through the phloem to rhizome sink tissues (glyphosate, synthetic auxin herbicides other than picloram), or targeted to the foliage and bare soil to directly disrupt and suppress growth above and belowground (picloram, synthetic auxin). Although no treatments were applied in summer (stage 1, Fig. 2), these would be directed toward emergent aboveground growth, depleting rhizome reserves.

The only treatments that showed significant reductions in *P. pyrenaicus* cover over the study period included annual spring (stage 4, Fig. 2) foliar application of glyphosate at FR (3.60 kg AE ha^{-1}) or HR (2.16 kg AE ha^{-1}), or soil and/or foliar application of picloram (1.34 kg AE ha^{-1}). We note that due to the residual activity of picloram in soil (at least one year; USDA Forest Service 2000), it can be applied throughout the calendar year (stages 1 to 4). Glyphosate was most effective where application timing was coupled to photosynthate flow to the rhizome (stage 4, Fig. 2). No significant control effect of foliar applied glyphosate at FR (3.60 kg AE ha^{-1}) was observed when resources are being mobilised to aboveground tissues in autumn (stage 2, Fig. 2). This highlights the importance of integrating species ecophysiology with perennial IAP management.

Prior to annual senescence in rhizome-forming plants (stage 4, Fig. 2), glyphosate is transported to metabolically active sink tissues during mass transit of photosynthate to the rhizome (Jones et al. 2018). Glyphosate accumulation within sink tissues (i.e., *P. pyrenaicus* leaf clump and rhizome buds (meristems) prevents regrowth in subsequent growing seasons by blocking indole-3-acetic acid (IAA) biosynthesis resulting in extensive localised cell and tissue death (Jiang et al. 2013; Gomes et al. 2014; Jones et al. 2018). The control effect of glyphosate is largely independent of dose, beyond a threshold application rate, because distribution across different tissues (i.e., leaf, petiole and rhizome) is determined by sink strength (Jones et al. 2018). Effective control can therefore be achieved at lower application rates i.e., glyphosate HR application rate (Gly., 2.16, Fol., Spr.; Table 1). Effective management using lower doses of glyphosate-based herbicide also optimises material and labour inputs. Based on our biological understanding of Japanese Knotweed (*R. japonica*; Jones et al. 2018), we propose that the *P. pyrenaicus* glyphosate application window may be extended to include the transitional phenological source-sink stage in winter (stage 3), increasing the potential application timeframe. Winter management of *P. pyrenaicus* could further enhance economic and environmental sustainability and minimise non-target effects of herbicide application because the plant is one of few species in leaf (and flower) in winter and would, therefore, be readily located.

We tested a range of synthetic auxin herbicides drawn from three chemical families: phenoxy-carboxylic acids (2,4-D amine), benzoic acids (dicamba) and pyridine-carboxylic acids (aminopyralid, clopyralid, fluroxypyr, picloram, triclopyr; Grossman 2009; Busi et al. 2017). The synthetic auxin herbicides tested did not significantly reduce *P. pyrenaicus* cover through depletion of rhizome reserves (stage 2, Fig. 2) and only picloram significantly reduced *P. pyrenaicus* cover via poisoning of rhizome buds/meristems (stage 4, Fig. 2). These results suggest that *P. pyrenaicus* synthetic auxin herbicide sensitivity is not based on chemical family, but rather it is the dose of herbicide active ingredient accumulated within rhizome buds/meristems which determines herbicide control efficacy.

Synthetic auxin herbicides mimic the main endogenous auxin (indol-3-acetic acid, IAA) and cause plant death by the overinduction of the auxin response leading to the deregulation of natural auxin regulatory mechanisms (Kelley and Riechers 2007; Grossman 2009). Tissue concentration of synthetic auxin herbicides is not determined by sink strength to the same degree as glyphosate-based herbicides and global accumulation *in planta* is proportional to herbicide dose (i.e., a classical dose-response relationship is observed; Streibig 2013). Meristematic tissues are most sensitive to synthetic auxin herbicides, and consequently these herbicides are highly effective at low application rates for the control of immature dicotyledonous weeds. In contrast, established, rhizome-forming plants possess a greater number of larger and more structurally robust meristems that allow rapid regeneration following disturbance (Ott et al. 2019). Consequently, a greater dose of herbicide must accumulate globally to poison these structures effectively. Picloram is effective for *P. pyrenaicus* control because it is persistent in the soil and remains in contact with rhizome meristems at sufficiently high concentration (and duration) to cause tissue accumulation and poisoning. Conversely, at the doses tested, foliar application of the other synthetic auxin herbicides was ineffective presumably due to insufficient accumulation within meristematic tissues (Krzyszowska et al. 1994; USDA Forest Service 2000).

Integration of winter excavation with spring glyphosate application (Exc+Gly., N/A+3.60, Fol., Win.+Spr.; Table 1) did not reduce *P. pyrenaicus* canopy cover in the long-term, despite greater labour and equipment requirements and cost, compared with the application of glyphosate alone. We suggest that this is due to disruption/damage of emerging aboveground tissues, reducing source tissue (leaf) strength and subsequent glyphosate translocation to active rhizome buds/meristems. Moreover, as clonality is a common adaptation to physical disturbance (Harper 1977; Ott et al. 2019) this management approach may be counter intuitive for invasive, rhizome-forming species. Physical covering (Covering, N/A, Win.; Table 1) was ineffective at controlling aboveground *P. pyrenaicus* canopy cover, indicating that long-term depletion of rhizome resources to achieve successful control is unfeasible. Physical covering is the only practical physical control treatment that can be applied at scale; other treatments such as pulling and cutting are too costly, labour intensive and likely to increase the risk of *P. pyrenaicus* spread.

Due to difficulties in obtaining accessible field sites of sufficient size, we acknowledge the relatively limited replication within our experimental design. However, we suggest that our long-term field-scale evaluation approach, incorporating multiple herbicide products and active ingredients, provides more realistic management data than short-term (less than 2 growing seasons) pot- and/or field-based experiments. This is because short-term experimental designs may overextrapolate the efficacy of treatments which disrupt aboveground growth (e.g. cutting, certain synthetic auxin herbicides) and conversely, do not detect the long-term efficacy of treatments that display limited aboveground control effects (symptomology), but are effectively poisoning belowground tissues (i.e., glyphosate-based herbicides; Child 1999; Skibo 2007; Jones et al. 2018). Where insufficient empirical data is available to underpin control of invasive plant populations, resulting ineffective management strategies are frequently characterised by excessive herbicide and labour inputs, and herbicide resistance may develop (Hutchinson et al. 2007; Kettenring and Adams 2011).

While we welcome trends toward less toxic and persistent active ingredient(s) contained within plant protection products (PPPs), continued reduction of the number of PPPs in Europe presents challenges for the effective management of rhizome-forming IAPs such as *P. pyrenaicus*, particularly in non-agricultural settings (Myers et al. 2016; Kudsk and Mathiassen 2020). Rhizome-forming IAPs have few weak points that can be exploited for management and, as the limited range of effective tools for their management continues to decline, so too does the likelihood of effective management at the landscape scale. Consequently, withdrawal of glyphosate for the control of invasive plants such as *P. pyrenaicus* could impact negatively upon native biodiversity (particularly in areas of nature conservation) and result in the application of ineffective and unsustainable (CO_2 intensive) management practices, to the detriment of wider ecosystem services (Pergl et al. 2020). Therefore, it is timely to encourage the development of new herbicide products targeting source-sink dynamics to increase the range of effective management tools for rhizome-forming invasive plants.

Conclusions

Management of rhizome-forming IAPs such as *P. pyrenaicus* is increasingly being undertaken across a range of sectors to minimise their long-term environmental and economic impacts. However, there is often limited scale-appropriate empirical evidence to support the selection of appropriate control methods, hampering effective management. Knowledge of treatment application timing and appropriate herbicide mode of action are the most important factors for the successful control of *P. pyrenaicus*. Multiple-stage glyphosate- and picloram-based treatments applied at the appropriate phenological stage (Fig. 2) were found to be most effective, completely controlling aboveground *P. pyrenaicus* growth (leaf canopy cover reduced to 0%). However, no control treatment completely eradicated *P. pyrenaicus* within four years of the first treatment application. Picloram was withdrawn from the European market in 2015, leaving glyphosate as the only effective control treatment for the management of *P. pyrenaicus* in much of the introduced range. We recommend that ineffective synthetic auxin herbicides and physical control methods (covering, cutting), that add equipment and labour costs and increase environmental impacts (CO_2 emissions) without improving control compared to spraying alone, are discontinued. While reduced herbicide application to control *P. pyrenaicus* can be achieved by targeted application, alternative control methods currently do not provide viable mitigation against the long-term deterioration of persistently invaded habitats.

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Supplementary material 1

Desk-based site geological, hydrological and historical surveys

Authors: Daniel Jones, Mike S. Fowler, Sophie Hocking, Daniel Eastwood

Data type: Docx file.

Explanation note: Geographical, geological, hydrological, current and historic landuse data for the Invasives Research Centre (IRC), Taffs Well.

Link: https://doi.org/10.3897/neobiota.74.82673.suppl1

Supplementary material 2

Field trial site treatment group assignment

Authors: Daniel Jones, Mike S. Fowler, Sophie Hocking, Daniel Eastwood

Data type: Docx file.

Explanation note: Schematic of field trial at the Invasives Research Centre (IRC), Taffs Well.

Link: https://doi.org/10.3897/neobiota.74.82673.suppl2

Supplementary material 3

***Petasites pyrenaicus* field trial herbicide properties, manufacturers and suppliers**

Authors: Daniel Jones, Mike S. Fowler, Sophie Hocking, Daniel Eastwood

Data type: Docx file.

Explanation note: Field trial herbicide properties, manufacturers and suppliers.

Link: https://doi.org/10.3897/neobiota.74.82673.suppl3