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Influence of Disturbance on Japanese Knotweed (*Fallopia japonica*) Stem and Rhizome Fragment Recruitment Success within Riparian Forest Understory

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ABSTRACT: Japanese knotweed (*Fallopia japonica*) is an herbaceous invader in North America and Europe with the ability to recruit via several modes (seeds, rhizome, and stem fragments). Within US riparian forests where Japanese knotweed invades, disturbances are common over space and time in the form of flooding and mowing. It remains unknown how disturbance influences the relative recruitment success of sexual and clonal propagules of this riparian invader. Using an experimental approach, we addressed this topic by planting seeds, and rhizome and stem fragments into riparian forest plots with intact Japanese knotweed subcanopies, and into plots with the Japanese knotweed subcanopy removed, simulating disturbance. We monitored canopy openness and propagule fate (shoot emergence and height) over five months. Regardless of treatment, rhizome fragments had a higher establishment probability (85%) than seeds (3%) or stem fragments (16%). Due to a small sample size, we did not analyze the effect of disturbance on seedling recruitment. Disturbance had little effect on the establishment of rhizomes and stems. Disturbance had a significant effect on the size and timing of shoot death from rhizome and stem fragments. During the fall we observed an earlier die-back of shoots from rhizomes in undisturbed treatment plots compared to disturbed treatment plots. Shoot height from rhizome and stem fragments was greater in undisturbed treatments than in disturbed. Our findings are limited to clonal propagules of Japanese knotweed but suggest that disturbance does not increase recruitment or propagule performance.

Index terms: Clonal reproduction, disturbance, *Fallopia japonica*, knotweed, sexual reproduction

INTRODUCTION

Many native and exotic plants within forest understories have the ability to recruit via the production of both clonal and sexual propagules (e.g., Bierzychudek 1982; Auge and Brandl 1997). Propagules are any plant unit with the potential to propagate, that is, to produce a new individual. Clonal propagules can be created through several processes, including the fragmentation of rhizomes, stolons, and stems, as well as the formation of tubers and bulbs. It is often true that compared to sexual propagules, seeds and seedlings (small plants derived from seeds), clonal propagules begin life at a more advanced stage with greater energetic reserves, allowing for increased survivorship and the ability to recruit in harsher habitats (Abrahamson 1980; Burt 2000; Francis et al. 2008). Conversely, sexual propagules typically have limited nutrient reserves and often require prime conditions to survive and photosynthetically build carbon stocks (Hartnett and Bazzaz 1985; Araki and Kunii 2012). The mixed reproductive strategy of producing sexual and clonal propagules has been observed in many invasive plants including Japanese knotweed (*Fallopia japonica* Houtt.) (Beerling et al. 1994), *Rosa multiflora* Thunb. (Jesse et al. 2010), *Ranunculus reptans* L. (van Kleunen et al. 2002), *Pueraria lobata* Willd. (Pappert et al. 2000), and *Phragmites australis* (Cav.) Steud. (Kettenring et al. 2011). An explanation for

the prevalence of this mixed reproductive strategy is that sexual and clonal propagules may be adapted for different suites of biotic and abiotic conditions, thereby together affording a broader recruitment niche than would be possible with either propagule type exclusively (Burt 2000). However, our understanding of the impact of environmental conditions on the relative recruitment success of sexual and clonal propagules remains woefully incomplete. Greater understanding of this topic, specifically among invasive plants, could aid managers seeking to prevent or limit the recruitment of problematic species.

We chose to use the riparian invader Japanese knotweed, *Fallopia japonica* (Houtt.) Ronse Decr., to investigate the impact of disturbance on sexual and clonal recruitment success. Japanese knotweed is native to Asia where it is typically found in early successional habitats (Adachi et al. 1996). A herbarium specimen of Japanese knotweed from New York in 1873 is the earliest record in the United States (Barney 2006). Within its introduced ranges in Europe and North America, Japanese knotweed populations establish in disturbed habitats such as along roadsides and riparian forest (Beerling et al. 1994). Over time they can form monodominant stands, which can decrease native biodiversity (Gerber et al. 2008; Urgenson et al. 2009; Stoll et al. 2012). Improving our understanding of the relationship between Japanese knotweed

establishment and disturbance may aid land managers focused on preventing Japanese knotweed recruitment and spread.

Japanese knotweed recruitment is complicated by the presence of multiple propagule types (seeds, rhizome and stem fragments), which may vary over time and space in their production and recruitment success. The breeding system of Japanese knotweed has been described as dioecious or gynodioecious (Beerling et al. 1994). Within its native range, Japanese knotweed reproduces both clonally via rhizomes and stems, and sexually (Maruta 1976). Populations of Japanese knotweed in the United Kingdom are composed solely of female plants, produce seeds only rarely, and those seeds may be sired from related taxa (*Fallopia sachalinensis* (Schmidt) Ronse Decraene, *Fallopia baldschuanica* (Regel) Holub, *Fallopia* × *bohemica* (Chrték and Chrtková) Bailey) (Bailey et al. 2009). Regions within the United States have documented the production of viable seeds (Forman and Kesseli 2003; Gammon et al. 2007). Under laboratory conditions it has been found that seeds from Japanese knotweed populations in Massachusetts displayed high germinability (>50%), with 50% of individuals reaching adulthood in greenhouse conditions (Forman and Kesseli 2003). In addition, overwintering of seeds in the soil does not decrease germination success, opening the possibility that a persistent seed bank may exist for this species (Engler et al. 2011). Within the Susquehanna River Basin, females often produce an abundance (hundreds to thousands) of achenes containing seeds with high germinability under laboratory and greenhouse conditions (C. Gowton, pers. obs.). In addition to seeds, Japanese knotweed can be propagated by small fragments of stems and rhizomes (De Waal 2001; Sásik and Pavol 2006). As long as the fragments contain a meristematic node, sprouting can occur in fragments less than 1 g (De Waal 2001; Sásik and Pavol 2006). Generally, little is known about the relative success of Japanese knotweed's three recruitment modes, but the few data that are available indicate that recruitment via rhizome fragments is more common than recruitment via seeds (Brock et al. 1995; Alberternst and Böhmer 2011). However,

it is unknown whether the habitat heterogeneity within riparian forests influences the recruitment performance of Japanese knotweed sexual and clonal propagules equally.

The light environment within the understory of riparian forests may differently affect the relative recruitment success of clonal vs. sexual propagules. Understory light variability may be influenced by natural disturbances, including, but not limited to, wind-throws, floods, and bank erosion (Moore and Richardson 2012). Anthropogenic disturbances, such as mowing and herbicide application, are common within Japanese knotweed invaded sites. Disturbance may increase canopy openness and light transmittance total (global site factor), allowing a greater proportion of light to reach the subcanopy and forest floor (Valverde and Silvertown 1997; Peterson et al. 2013). Global site factor (GSF) is the proportion of solar radiation reaching a fixed point. This measurement takes into account both direct and diffuse solar radiation to give a measure of total percent light transmittance. Global site factor has been positively correlated with the establishment of sexual propagules—seed germination and seedling survival (Myer and Schmid 1999; Kanno and Seiwa 2004; Matlaga and Horvitz 2009; Li et al. 2011), and the growth of clonal propagules (Morris et al. 2004; Rasheed 2004). In undisturbed forests, clonal offspring may show greater relative recruitment success compared to seedlings due to the high light requirements of some seedlings (Kanno and Seiwa 2004; Matlaga and Horvitz 2009; Li et al. 2011).

Our goal was to determine how simulated disturbance (knotweed removal in conjunction with surface soil raking) affects the understory light environment of the riparian forest and, consequently, the relative recruitment success of Japanese knotweed clonal and sexual propagules. We hypothesized that (1) rhizome fragments will have higher recruitment than seeds or stem fragments, (2) recruitment for all propagule types will be greater in disturbed compared to intact Japanese knotweed stands, and (3) emerging shoots will be taller within the disturbed stands

compared to undisturbed stands.

METHODS

Study Sites

Using an experimental approach, we observed the recruitment success of three Japanese knotweed propagule types (rhizome fragment, stem fragment, and seeds) in disturbed and undisturbed plots (from here after “recruitment plots”) within riparian forest. We conducted our field experiment from 6 June 2013 to 20 October 2013, replicated at three sites along the west bank of the Susquehanna River in Snyder County, Pennsylvania (Isle of Que 40°78' N, 76°85' W; Fabri Dam Park 40°85' N, 76°81' W; and Sunbury Power Plant 40°84' N, 76°82' W). Sites were at least 430-m apart. The tree canopy at our sites consisted mainly of silver maple (*Acer saccharinum* L.) and sycamore (*Platanus occidentalis* L.). Japanese knotweed was the dominant understory species at our sites but Jewelweed (*Impatiens capensis* Meerb.) and Poison Ivy (*Toxicodendron radicans* (L.) Kuntze) were also present. We were unable to investigate recruitment into areas unoccupied by Japanese knotweed due to the scarcity of uninhabited sites in our area.

Establishment of Recruitment Plots

We collected rhizomes, shoots, and achenes at our three sites. During the week of recruitment plot establishment, we unsystematically collected 240 rhizome and stem fragments. Rhizomes connected to living shoots were excavated to an approximate depth of 30 cm, severed, and rinsed to remove soil. We collected living stems and unsystematically cut them into varying lengths using hand shears with the goal of having an equal number of stem fragments with 1–3 nodes. The weight of each rhizome and stem fragment was recorded. In February 2013, we collected mature Japanese knotweed achenes and stored them at room temperature.

At each of the three sites, we established eight recruitment plots (four disturbed,

four undisturbed). Pretreatment, the understory of the recruitment plots was a near monoculture of Japanese knotweed with a very small number of woody stems. The herbaceous layer was extremely sparse, with only a few individuals of the Poaceae, Juncaeaceae, and *Impatiens* (Balsaminaceae) present. Our disturbance treatment was intended to mimic a mechanical disturbance that knocks down noncanopy vegetation and disturbs the soil surface (i.e., mowing, off-road vehicle use). Disturbed recruitment plots experienced removal of all aboveground biomass (both herbaceous and woody) <5 cm DBH by cutting the vegetation at the soil surface with hand shears. After vegetation removal, we disturbed the soil surface by raking using a rake with 4-cm steel tines. The forest overstory, consisting mainly of silver maple and sycamore, was not manipulated. We applied the disturbance treatment within a 2.5-m radius circle. The vegetation and soil surface remained intact in undisturbed recruitment plots. It is not logistically feasible, or realistic, to disturb the soil surface underneath the dense Japanese knotweed canopy without also disturbing the vegetation; therefore, we did not establish a third treatment of raking without vegetation removal.

Propagules were planted into a rectangular 2.5 × 2-m recruitment plot consisting of six rows of five planted propagules (30 propagules per plot: 10 seeds, 10 rhizome fragments, and 10 stem fragments). Propagules were planted under a thin layer of soil (>1 cm). Propagule types were randomly assigned to locations (unique row, column combinations). Across all three sites, there were 120 individuals of each propagule type per treatment. In the disturbance treatment the rectangular recruitment plot was located inside of the circular area where the treatment was applied. Rhizome and stem fragments were marked with fluorescent pink flagging tape exposed at the soil surface to distinguish from natural reproduction of existing plants. All propagules received an identification tag in order to keep track during censusing.

Each propagule was censused every 28 days over a 112 day period. At each census, we recorded the presence or absence of

aboveground shoots. If shoots were present, we loosely marked the shoot with flagging tape and measured shoot height from the ground to the tip of the terminal leaf.

To quantify canopy openness or percent light transmittance total, a proxy of understory light availability, we utilized hemispherical photography to take photographs of the tree canopy directly above propagules using a digital camera (Nikon Tokyo, Japan Coolpix 4500, with a Nikon FC-E8 with a fisheye converter lens (180° field of view)). Canopy photos were taken above a randomly selected propagule within each row of each plot (six pictures per plot). During recruitment plot establishment hemispherical photographs were taken 10 cm above the newly planted propagules. At each consecutive census, hemispherical photographs were taken at terminal leaf height if the propagule had shoots, or 10 cm above the soil surface if no shoots were present. We then analyzed hemispherical photographs to obtain percent transmittance total, or global site factor (GSF, defined in the Introduction) utilizing Gap Light Analyzer 2.0 (Canham 1995).

Statistical Analyses

Statistical analyses were conducted using SPSS (IBM SPSS Statistics for Windows, Version 22.0. Armonk, NY, IBM Corp.). Differences in GSF among treatments and over time were analyzed using a repeated measures ANOVA ($\alpha = 0.05$) with treatment as the independent variable and time as a covariate. Separate logistic regressions were used to analyze the effect of treatment (independent variable) and propagule weight (covariate) on establishment (produced aboveground shoot or did not) and shoot death (shoot died during study period or did not) of rhizome and stem fragments. Analysis of Covariance (ANCOVA) was used to determine the effect of treatment (independent variable) and propagule weight (covariate) on shoot height (dependent variable) from both stem fragments and rhizome fragments. We log transformed the weight of stem fragments and rhizome fragments, used as a covariate, to meet the assumption of normality in all statistical analyses.

RESULTS

Effect of Simulated Disturbance on Global Site Factor

Our simulated disturbance treatment significantly increased global site factor (GSF) by over 17% compared to the undisturbed treatment (Table 1; Figure 1). GSF changed significantly over time and the pattern of change in GSF differed significantly between treatments, indicated by a significant treatment by time interaction (Table 1). Overall GSF within disturbed treatments displayed a parabolic pattern whereas GSF within undisturbed treatments continually increased over time (Figure 1). Both disturbed and undisturbed treatments experienced an increase in GSF beginning 84 days after the experiment began (Figure 1), corresponding with the loss of canopy leaves during the onset of the fall season.

Effect of Simulated Disturbance on Shoot Emergence, Height, and Death

The majority of shoot emergence occurred within 28 days after the propagules were planted (Figure 2). Rhizome fragments had the highest proportion of propagules with emerging shoots followed by stem fragments and then seeds. Overall, the proportion of rhizomes with emerging shoots was over five times greater than that of stem fragments and over 28 times greater than that of seeds, across treatments. Due to the small sample size of emerging shoots from seeds (8 total: 7 in disturbed and 1 in undisturbed treatments) statistical analyses could not be conducted for this propagule type. The occurrence of shoot emergence was equal between disturbed and undisturbed treatments for both stem and rhizome fragments (Table 2). The probability of shoot emergence increased significantly with propagule weight for rhizome fragments but not for stem fragments (Table 2).

Patterns of shoot death differed between shoots produced by rhizome and stem fragments. Shoot death commenced during the second census or 56 days after planting (Figure 2). The proportion of

Table 1. Repeated Measures analysis of percent transmittance total, or global site factor (GSF) between treatments (simulated disturbance vs. no simulated disturbance) over the 112-day study period. *P* values less than 0.05 are in bold.

Factor	Type III Sum of Squares	df	MS	<i>F</i>	<i>P</i>
Between-subject effects					
Treatment	21265.4	1	21265.4	728.3	<0.001
Error	2481.9	85	29.2		
Within-subject effects of time					
Time	2194.719	2.7	820.8	41.3	<0.001
Time × Treatment	1350.1	2.7	504.9	25.4	<0.001
Error (Time)	4516.1	227.3	19.9		

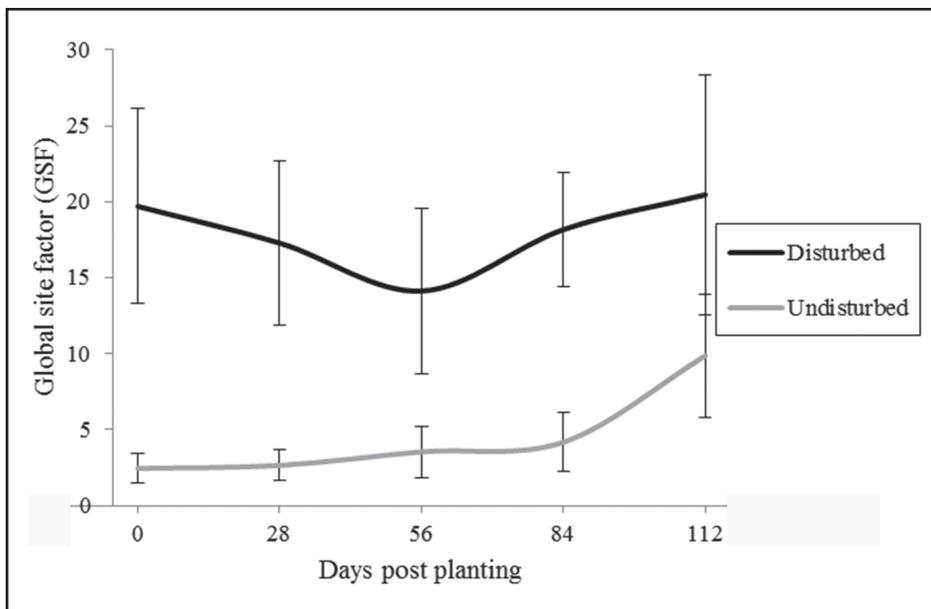


Figure 1. Average percent transmittance total, or global site factor (GSF) calculated from hemispherical photographs taken above disturbed (black) and undisturbed (grey) treatments. Error bars display 1 standard deviation.

shoots dying was equal between treatments for stem fragments, with over 70% death at the conclusion of the experiment. A greater proportion of shoots produced from rhizome fragments had died during the study period in the undisturbed treatment compared to the disturbed treatment (Figure 2; Table 2). Rhizome fragment weight did not influence the occurrence of shoot death nor did initial stem weight for shoots emerging from stem fragments (Table 2).

There was a positive relationship between

propagule weight at the time of planting and maximum shoot height for both rhizome fragments and stem fragments (Figure 3; Table 3). The disturbance treatment significantly influenced the maximum shoot height for rhizome fragments but not stem fragments (Table 3). Shoots produced by rhizome fragments were significantly taller within the undisturbed treatment compared to those in the disturbed treatment (Figure 3A; Table 1). The interaction term between treatment and propagule weight did significantly affect shoot height for rhizome and stem fragments (Table 3).

DISCUSSION

Japanese knotweed is spreading in riparian habitats within its exotic range in the United States and Europe where it has been shown to impact plant communities (Gerber et al. 2008; Urgenson et al. 2009; Stoll 2012), invertebrate communities (Gerber et al. 2008; Stoll 2012), and some ecosystem processes (Urgenson et al. 2009). Despite the prevalence of this invader and the potential severity of its impacts, little information is available to indicate which factors impact the recruitment success of Japanese knotweed in the field. Our study is the first to compare the recruitment potential of Japanese knotweed's three propagule types (rhizome fragments, stem fragments, and seeds) in response to disturbance. Our results clearly indicate that within the riparian forest understory conditions we studied, these propagule types have distinct recruitment potentials. However, our simulated disturbance treatment had, at most, only a minor influence on the recruitment of Japanese knotweed via any of the three propagule types. Clonal recruitment, via both rhizome and stem fragments, was unaffected by disturbance; however, disturbance did influence shoot behavior postrecruitment.

There has been speculation and discussion surrounding the occurrence and consequence of sexual reproduction among Japanese knotweed within its exotic range (Bailey et al. 2009). In parts of Europe, all *Fallopia japonica* individuals are

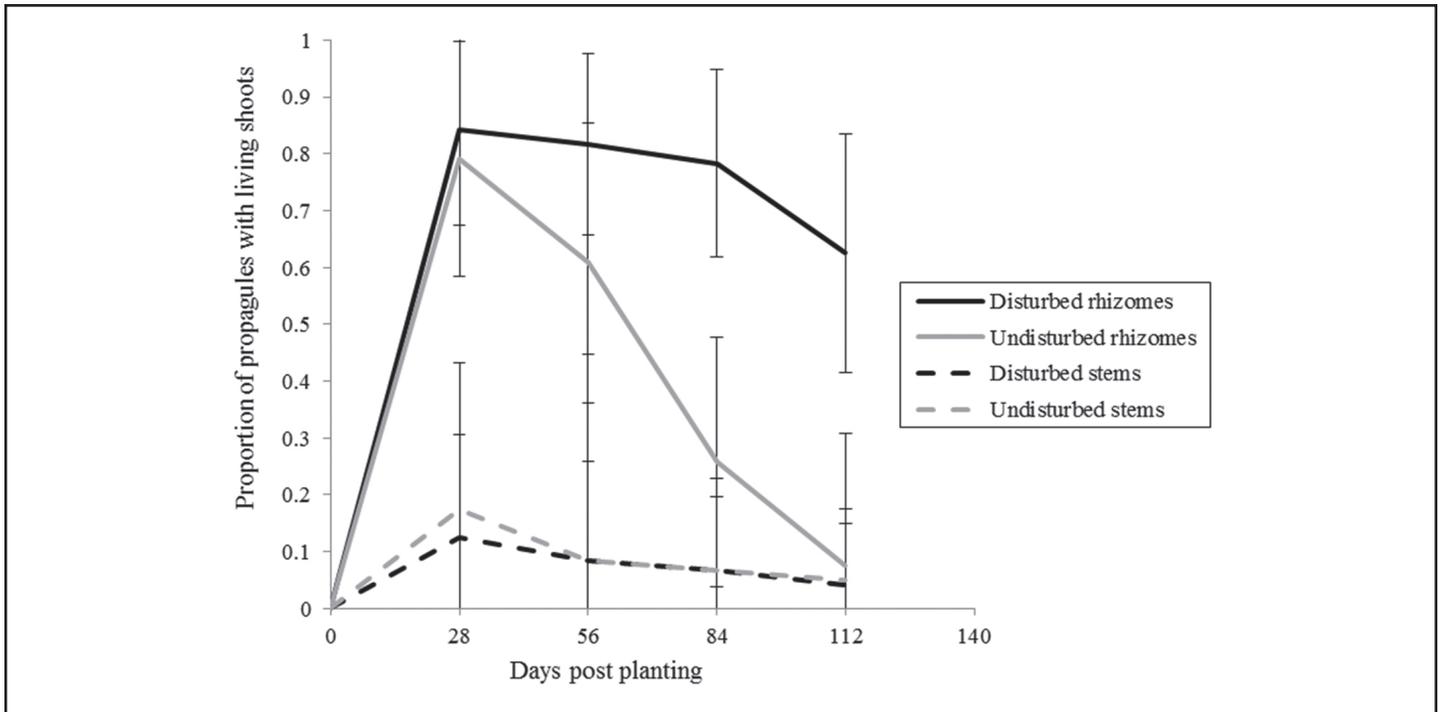


Figure 2. Proportion of propagules—rhizome fragments (solid line) and stem fragments (dashed line)—with living shoots within disturbed (black) and undisturbed (grey) treatments. Error bars display 1 standard deviation.

an identical female clone, which rarely produces seeds and those seeds that are produced are sired by other *Fallopia* species (Grimsby 2007). It is thought that in these circumstances, *F. japonica* spreads exclusively via clonal recruitment. Initially it was assumed that US populations were similar to those in Britain, having little to no sexual reproduction (Grimsby 2007). However, within many locations in the United States, including our region of study, female Japanese knotweed ramets

produce hundreds to thousands of fruits (D. Matlaga, pers. obs.). Genetic diversity data collected in wild US populations indicate that successful recruitment of sexually produced offspring does occur (Grimsby et al. 2007). Seedling recruitment rates observed in our study were lower than those observed in comparable other studies. Bram and McNair (2004), using a buried bag field study conducted in Pennsylvania, found germination rates ranging from 55%–92%. Seeds collected in German

populations and placed on filter paper in petri dishes under laboratory conditions had 24%–91% germination (Engler et al. 2011). Forman and Kesseli (2003) placed seeds collected from Massachusetts in soil under laboratory conditions and found 30% seedling emergence.

The low seedling emergence rates we observed are not likely due to low seed viability within our seedlot. Viability of our seedlot was assessed both before and

Table 2. Logistic regression analysis of the effect of treatment (simulated disturbance vs. no simulated disturbance) and propagule weight (covariate) on shoot emergence and subsequent shoot death for both rhizome and stem fragments. Propagule weight was log transformed to conform with the assumptions of normality. *P* values less than 0.05 are in bold.

Propagule	Dependent variable	Factor	SE	Wald X^2	df	<i>P</i>
Rhizome	Shoot emergence	Treatment	0.4	0.1	1	0.767
		Weight (covariate)	0.2	11.6	1	0.001
	Shoot death	Treatment	0.3	51.3	1	<0.001
		Weight (covariate)		0.2	1	0.671
Stem	Shoot emergence	Treatment	0.4	2.1	1	0.145
		Weight (covariate)	0.2	4.5	1	0.34
	Shoot death	Treatment	0.4	1.8	1	0.18
		Weight (covariate)	0.2	1.5	1	0.218

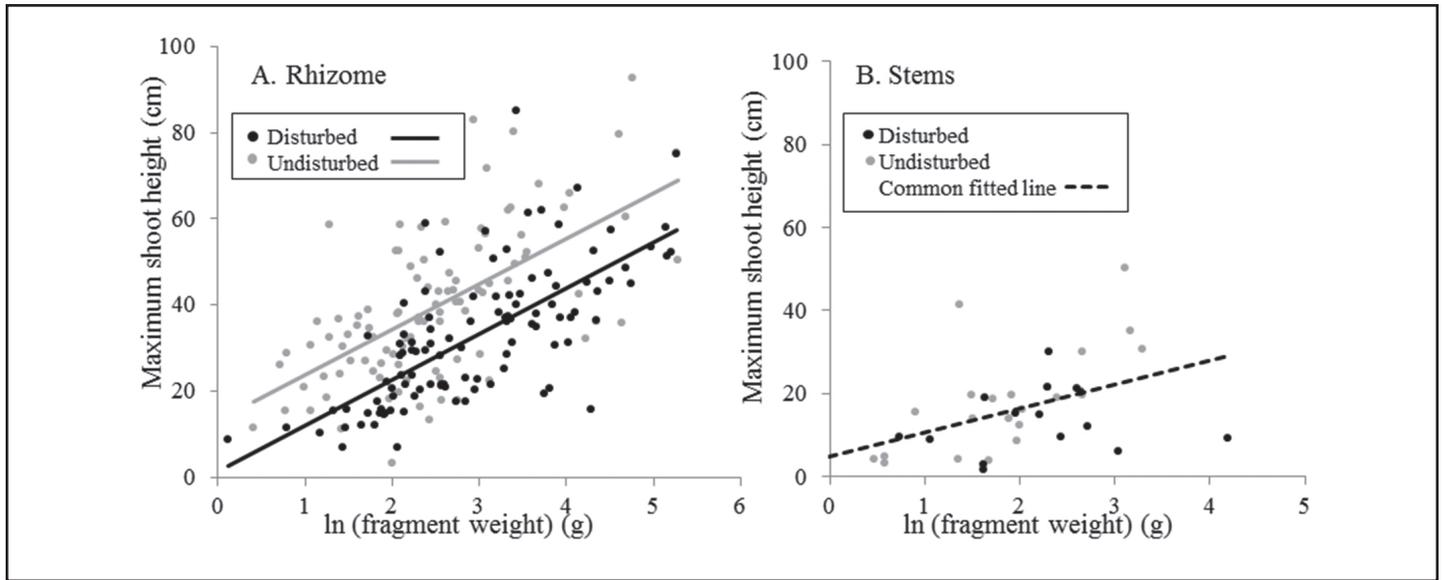


Figure 3. Relationship between propagule weight at the time of planting (natural log) and maximum shoot height for rhizome fragments (A) and stem fragments (B). Lines of best fit added for disturbed (black) and undisturbed (grey) treatments for shoots originating from rhizome fragments (A). A line of best fit (black) was added to represent both disturbed and undisturbed treatments since there was no significant difference between treatments.

after the initiation of our experiment. In a related study conducted prior to our field experiment, seedling emergence of our seedlot was studied in pots containing field soil within an environmental chamber in February 2013. Seedling emergence was 54% (A. Budsock, unpubl. data). After our experiment, germination of the seedlot was assessed in April 2014 by placing seeds on filter paper in petri dishes within a growth

chamber. Under these conditions 44% of seeds germinated (C. Gowton, unpubl. data). Due to the relatively high germination rates in these related experiments, we expected to observe relatively consistent results in our present study. There are several potential explanations for the low germination rates we observed in the field. Seeds may have been washed away during rain events due to their small size and the

shallow depth they were planted. Forman and Kesseli (2003) observed that marked Japanese knotweed seedlings were quickly overtaken by established knotweed plants and could not be found after one month. We observed resprouting from established rhizomes within our disturbed plots, which may have overtaken seedlings. Alternatively, seeds may not have germinated due to a mismatch in field conditions and the

Table 3. ANCOVA results investigating the effect of propagule weight (covariate) and treatment on shoot height. Propagule weight was log transformed to conform with the assumptions of normality. *P* values less than 0.05 are in bold.

Propagule	Factor	Type III SS	df	MS	<i>F</i>	<i>P</i>
Stem	Intercept	85.7	1	85.8	1.1	0.298
	Treatment	123	1	123	1.6	0.214
	Weight	1159.5	1	1159.5	15.1	<0.001
	Treatment × weight	459.3	1	459.3	6	0.020
	Error	2682.5	35	76.6		
	Total	14817.8	39			
Rhizome	Intercept	1417.2	1	1417.2	9.1	0.003
	Treatment	858.7	1	858.7	5.5	0.020
	Weight	24877.6	1	24877.6	158.9	<0.001
	Treatment × weight	0.1	1	0.1	0.001	0.982
	Error	31631.5	202	156.6		
	Total	325975.8	206			

safe-site conditions for this species. This explanation is difficult to evaluate due to the scarcity of data on the germination requirements for this species.

Shoots emerging from rhizome fragments in the undisturbed treatment were taller than those emerging from rhizome fragments grown in the disturbed treatment. This pattern may be explained by the shade avoidance effect, where shading results in longer internode length (Huber and Wiggerman 1997; Nishimura et al. 2010; Zhang et al. 2014). The pattern of greater height under shaded conditions compared to higher light conditions has been observed in *Glycine max* L. (Zhang et al. 2014), *Chenopodium album* L. (Nishimura et al. 2010), and *Trifolium fragiferum* L. (Huber and Wiggerman 1997). We did not measure the existing Japanese knotweed stand height within this experiment. We observed that Japanese knotweed shoots regrowing in our disturbance treatment never reached the height of the knotweed shoots in our undisturbed treatment.

The influence of light heterogeneity on the onset of shoot death among recruits has received little attention in the literature. We observed an earlier onset of shoot death in undisturbed plots than in disturbed. This pattern may also be explained by the shade avoidance effect. Rhizome fragments in the undisturbed treatment may have exhausted their reserves earlier than those in the disturbed treatment by allocating more to growth.

We found that clonal recruitment of Japanese knotweed, via both rhizome and stem fragments, was unaffected by our simulated disturbance treatment. This is similar to other studies investigating the response of sexual and asexual recruitment to disturbance. For example, classic research on both *Solidago canadensis* L. and *Ranunculus repens* L. found that asexual recruitment of ramets was relatively insensitive to disturbance while genet recruitment occurred only within a specific time-since-disturbance window (Hartnett and Bazzaz 1985; Watkinson and Powell 1993). Clonal propagules may be insensitive, or buffered, from some environmental heterogeneity due to their higher quantities of energetic

reserves (i.e., stored carbohydrates) compared to seeds and seedlings (Abrahamson 1980; Burt 2000; Francis et al. 2008). Our results reporting the performance of severed rhizome fragments do not address how recruitment occurs in intact rhizome systems. Aguilera et al. (2010) performed a severing experiment on Japanese knotweed and showed that connectivity to the parental clone increases overall biomass production. Establishing rhizomes may be more dependent on parent resource sinks (carbohydrates stored in rhizome system) than on light availability. Our study, which only considered rhizome fragments that were severed from their parent plant, cannot address the importance that clonal integration may play in clonal recruitment. In addition, our disturbance treatment at best only mimics a mechanical disturbance (i.e., mowing). It does not mimic a disturbance that significantly influences nutrient availability (i.e., fire, flood).

Overall, rhizome fragments had a significantly greater probability of recruiting compared to stem fragments and seeds, in agreement with previous research, suggesting that rhizome fragments are the predominant mode of Japanese knotweed recruitment (Brock and Wade 1992; Brock et al. 1995). Furthermore, Colleran and Goodall (2014) observed postflooding recruitment of Japanese knotweed and found that 70% of recruits were rhizome fragments, and 30% were stem fragments. One obvious hypothesis for the contrasting recruitment success between seeds and clonal propagules is the large difference in propagule size. Japanese knotweed seeds are small (>0.002 g) compared to the smallest clonal propagule included in our study (0.38 g). Among clonal propagule types, we observed a positive effect of propagule weight on shoot height in shoots originating from rhizomes and stem fragments. Both Colleran and Goodall (2014) and Francis et al. (2008) observed taller Japanese knotweed shoots sprouting from larger stem and rhizome fragments. Our study utilized a larger range of rhizome fragment weights than Francis et al. (2008). One possible mechanism for this observed pattern is that heavier propagules contain larger quantities of essential nutrients for growth. Therefore, shoots originating from

larger clonal propagules may allocate those resources towards aboveground growth, whereas smaller propagules may have increased belowground growth to allow for increased nutrient uptake.

Our study contributes to the incomplete understanding of the recruitment behavior of this noxious invasive species within managed riparian forests. Management and control of Japanese knotweed in both the United States and Europe has been described as “extremely difficult, if not impossible” (Weston et al. 2005). The primary control strategy relies on repeated mowing of aboveground shoots because proximity to waterways often limits the use of herbicides (Baker 1988; Weston et al. 2005). Postmowing, it is recommended that the site be raked to remove stem fragments that could recruit (Seiger and Merchant 1997). Therefore, our disturbance treatments, which combined removal of aboveground material and raking, represent a good approximation of Japanese knotweed managed sites. Our results provide useful information for land managers concerned that this form of management may be creating ideal sites for knotweed recruitment. Our research suggests that Japanese knotweed would recruit into managed sites at the same rate it recruits into unmanaged knotweed stands, regardless of the propagule type. While our results suggest that Japanese knotweed recruitment is similar between cut and uncut treatments, research by Siemens and Blossey (2007) suggests that cutting knotweed may improve the recruitment of some native species. Siemens and Blossey (2007) found that the growth and survival of *Eupatorium perfoliatum* L. and *Acer saccharinum* was higher in areas where Bohemian knotweed (*F. × bohemica*) (Chrték and Chrtková) Bailey was cut at ground level compared to areas where Bohemian knotweed remained intact. In conjunction with repeated mowing, trenching to sever knotweed rhizomes that support new growth (Aguilera et al. 2010) may aid in controlling this species in some situations. In addition, our results demonstrate that establishment success increases with stem fragment size; therefore, ideally, knotweed stems should be shredded after mowing when possible. Clearly, future research is

needed to understand the recruitment niche of Japanese knotweed's three propagule types across the widest range of habitats. Specifically, elucidating the recruitment success of seeds, and stem and rhizome fragments across the light availability gradient from high light (roadside right-of-ways, river banks, etc.) to low light (under conspecifics) is needed.

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