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Toxic effects of knotweed *Polygonum cuspidatum* s.l. rhizome on the mosses *Atrichum angustatum* and *Thuidium delicatulum*

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Knotweed *Polygonum cuspidatum* s.l. is a large, suffrutescent, perennial forb native to northeastern Asia that was imported as an ornamental and has become a widespread invasive species in urban and rural environments of North America and Europe. Studies have demonstrated knotweed allelopathy to the germination and growth of many tracheophytes, but we have found no studies of knotweed toxicity to bryophytes. Therefore, the aim of this study was to determine if knotweed extracts affected the growth of the gametophytes of two mosses: *Atrichum angustatum* and *Thuidium delicatulum*. Both moss species were exposed to aqueous rhizome extracts of knotweed in concentrations of 0 (control), 10, 25, 50 and 75% for a total of nine days in the laboratory. All non-zero concentrations resulted in significant losses of green biomass, with the greatest losses occurring at the highest concentrations. Samples exposed to the three highest concentrations lost 80% of green mass after nine days. These results help explain the scarcity of moss growth on or near live knotweed crowns.

Keywords: *Fallopia japonica*, invasive species, invasiveness, *Reynoutria japonica*, roof mosses

In recent years, exotic tracheophytes have been linked to global decreases in biodiversity (Thuiller 2007). Within this category of exotic plants, the effects of each vary greatly (Pyšek and Richardson 2010). Whereas some exotics have little or no effect on native species diversity, others cause a considerable impact by altering ecosystem functioning and outcompeting native species for resources (Richardson et al. 2000, Grotkopp et al. 2002). Consequently, understanding why some exotic plants become invasive is crucial to limiting their spread and impact.

Japanese knotweed *Polygonum cuspidatum* Siebold & Zucc. = *Fallopia japonica* or *Reynoutria japonica* (hereafter 'knotweed') is an ornamental plant native to northeastern Asia that typically grows in dense colonies up to three meters tall in its nonnative range (Beerling et al. 1994). It is a widespread suffrutescent perennial considered to be one of the world's most invasive species due to its ability to form dense, highly dominant stands (Lowe et al. 2000). Knotweed and its relative giant knotweed *Polygonum sachalinense* F. Schmidt *ex* Maxim. and their hybrid Bohemian knotweed *Polygonum* × *bohemicum* [J. Chrtek & Chrtková] Zika & Jacobson exhibit some of the strongest impacts on species diversity of tracheophytes, reducing diversity, for example, by 66–86% in 4 × 4 m plots in the Czech Republic (Hejda et al. 2009). Knotweed is among the most-studied invasive plants (Pyšek et al. 2008); however, the mechanisms it utilises to achieve dominance are not fully understood. Some studies have attributed its success to a high growth rate (Marigo and Pautou 1998), ability to rapidly regenerate (Child and Wade 2000) and ability to grow at low nutrient levels (Adachi et al. 1996). Other research indicates allelopathy: the release of chemicals from leaves, litter or rhizomes through leaching, root exudation and residue decomposition (Kruse et al. 2000). These allelochemicals modify the environment of the plant and that of others growing in the vicinity (Nandal et al. 1994). Allelochemicals may inhibit shoot and root growth, nutrient uptake and seed germination as well as affect naturally occurring symbiotic relationships (Musyimi et al. 2012). Allelochemicals may not always affect nearby plants in a detrimental way and can either inhibit or stimulate other species (Jackson and Willemsen 1976, Musyimi et al. 2012). Allelopathy is currently considered an important factor in the spread and consolidation of certain invasive plants (Wang et al. 2011).

Knotweed has been shown to produce allelopathic effects on the germination and growth of a number of tracheophytes such as white mustard *Sinapis alba*, common nettle *Urtica dioica*, bushgrass *Calamagrostis epigejos*, garden cress *Lepidium sativum*, willow *Salix* sp. and eastern cottonwood *Populus deltoides* (Vrchotová and Šerá 2008, Moravcová et al.

2011, Dommanget et al. 2014, Gillies et al. 2016). There is evidence that tracheophytes can be allelopathic to mosses (Chaudhary and Kothari 2002, Natalia et al. 2008, Startsev et al. 2008, Halarewicz and Pruchniewicz 2015). To our knowledge, however, there has been no study of knotweed toxicity to mosses.

Mosses are important components of many ecosystems due to their abilities to reduce soil erosion and improve the soil's nutrient holding capacity (Cornelissen et al. 2007), as well as providing microhabitats for small organisms. In addition, they have applications as bioindicators of heavy metal deposition, air pollution and acid rain damage (Zechmeister 1998, Bignal et al. 2008). Low per cent cover of moss within knotweed stands has been reported in Europe (Chmura et al. 2015) and in New York (Kiviat unpubl.), but the reasons for moss scarcity beneath knotweed are unknown. Our study was engendered by the observation in Central Park, New York City, and in the northern Catskill Mountains, New York, of moss growth on dead but rarely on live knotweed crowns (Kiviat unpubl.). Knotweed stems are cespitose from a raised crown (sensu Lavallée et al. 2019), which can be at least 15 cm high and 30 cm in diameter (Kiviat unpubl.). Crown density can exceed 1.3 m^{-2} (Smith et al. 2007), suggesting the potential intensity of their influence on moss establishment. We chose to examine the effects of rhizome extracts (rather than leaf extracts) to represent this apparent effect of knotweed crowns on mosses.

Our preliminary experiment examined the potential role of toxicity in the suppression of mosses in knotweed-invaded habitats. We specifically aimed to determine whether knotweed could chemically inhibit growth of mature moss gametophytes under conditions of increasing knotweed leachate concentrations and exposure times. Two mosses, *Thuidium delicatulum* (Hedw.) Schimp. and *Atrichum angustatum* (Brid.) Bruch & Schimp., differ in growth habit and environmental tolerances. However, both can be found in light shade and somewhat dry or exposed conditions (Janice Glime, Michigan Technological Univ., pers. comm.). Knotweed in the northeastern US typically thrives in vacant urban spaces, road and railroad verges, stream banks, floodplains, wetland edges and dumps, in places beneath open canopy woodland, in dry or moist soil ranging from full sun to partial shade (Kiviat unpubl.). Knotweed tolerates saline or acidic soils, heavy metal contamination, fluctuating water levels and physical disturbance (Gillies et al. 2016, Kiviat unpubl.). Knotweed is robust, suffrutescent and in well-developed stands has large, well-spaced, elevated crowns, a dense leafy canopy from about 1 m to 3 m above the ground, and aboveground biomass up to 2000+ g m^{-2} dry weight (Kiviat unpubl.). Vigorous knotweed plants develop massive underground parts.

In the northeastern states, whether in urban or rural environments, mosses are rare beneath a knotweed canopy and on live crowns or stem bases. However, dead, decomposing knotweed crowns (or dead portions of live crowns) and intervening space in declining stands may be colonised by diverse mosses. We therefore decided to test whether aqueous extracts of knotweed rhizomes were toxic to mosses.

Material and methods

Acquisition and preparation of mosses

Moss material was obtained from Mountain Moss Enterprises (certified by the state of North Carolina to distribute live moss plants through its nursery operations – NC Licence/Certification #6440). The moss was delivered in plastic trays, with little soil attached to the rhizoids, and appeared healthy. Upon arrival, samples were lightly squeezed to remove excess water, then air-dried for six days until the material was brittle and dry to the touch. Mosses in general, and *Thuidium delicatulum* specifically, tolerate drying and rehydration well (Martin and Warner 1984), thus we did not expect this treatment to affect the experiment.

Collection of knotweed rhizomes

Genetic studies (Gammon et al. 2007) indicate that much northeastern knotweed is a hybrid swarm. We do not distinguish *Polygonum cuspidatum* from morphologically similar *P.* × *bohemicum*, hence our 'knotweed' can be considered *Polygonum cuspidatum* s.l. Vrchotová and Šerá (2008) found similar allelopathic effects of the two parents and the hybrid on germination of white mustard. We collected live rhizomes from a well-developed knotweed stand located on Mohonk Road (Route 6), New Paltz, New York (41°46′43.93″N, 74°08′05.8″W) in July and August 2016. The stand appeared healthy with no obvious damage. A voucher specimen of leafy branches has been deposited in the Bard College Field Station Herbarium. Five medium-sized living rhizome sections were collected in July for a preliminary dilution series and 13 medium-sized rhizome sections were collected in August for the experiment. Debris and soil were removed from the rhizomes by gently shaking and spraying with distilled water. Rhizomes were then used promptly to create aqueous extracts.

Creation of aqueous rhizome extracts for preliminary testing

We endeavoured to mimic the exposure of mosses to rain-leached knotweed allelochemicals by means of aqueous extracts of knotweed rhizome in the laboratory. A preliminary dilution series experiment was run utilising garden cress *Lepidium sativum* to determine concentration levels for the moss experiment (this species has been used in other allelopathy assays, Bousquet-Mélou et al. 2005). Knotweed rhizome was cut into pieces ca 6 cm long, and the pieces oven-dried at 60°C for 1 h, yielding 1345 ml dry volume of rhizome. From this, 0 (control), 1, 3, 5, 10, 25, 50, 75 and 100% solutions were created. Appropriate volume/volume ratios of knotweed and distilled water were pulverised in a blender; the mixtures were soaked for 24 h to make 500 ml graded dilutions. Thus, to create the 50% dilution, for example, 250 ml of knotweed and 250 ml of distilled water were blended, and for the 10% dilution, 50 ml of knotweed were blended with 450 ml of water. Solutions were placed in containers, labeled and sealed. They were stirred and aerated daily, and the cress trial was performed after four days.

Ten garden cress seeds were planted in each slot of a seedling tray. Each concentration was assigned eight slots. For four days, samples were each watered with 10 ml of designated extract using a graduated transfer pipette. After four days, number of seeds germinated out of 10 was recorded for each slot. Mean seed germination, standard deviation and standard error were calculated for each concentration. It was determined that 10% was the lowest aqueous extract that would have an effect, based on its mean and standard deviation. Thus, for the actual experiment, aqueous extract concentrations of 0 (water control), 10, 25, 50 and 75% were used.

Creation of extracts for experiment

Extracts were prepared as for the preliminary series. The total volume of dried rhizome cuttings was 2880 ml. From this, 0, 10, 25, 50 and 75% extracts were created, each 1800 ml in volume. Solutions were stored for 1 day prior to the experiment. Inasmuch as we did not know the magnitude of effect on mosses to expect, and in keeping with the cress trial, we chose to use a wide range of extract concentration (Musyimi et al. 2012).

Three day exposure of mosses

After drying for six days, the moss material was exposed to the knotweed extracts. Forty plastic petri dishes were filled with sterile planting soil, 20 for each moss species. Five concentrations of extract (0, 10, 25, 50 and 75%) were tested. Each moss had four replicates of each concentration. Dried *Atrichum angustatum* and *Thuidium delicatulum* were planted in each dish (5.0 g and 3.0 g of moss, respectively). The unfiltered extracts were applied beneath the mosses to mimic the effect of mosses growing on knotweed crowns. Each petri dish was labeled with species, concentration of extract and a sample number. Each moss sample was rehydrated by watering with 15 ml of designated extract daily for three days. After the three day exposure period, all moss samples were removed from their dishes. Excess soil and moisture were removed from the samples, and samples were manually fragmented. Fragments that were brown to black were considered dead, whereas fragments that were vibrant green to slightly yellow were considered to be alive. Brown or black material was discarded, and green biomass was spread on paper envelopes designated for each dish. The green moss material was air-dried for two days at ca 24°C after which mosses were dry and brittle to the touch. Each sample was then weighed to the nearest 0.1 g on an electronic balance. Extract preparation and experiments were conducted in partial shade at ca 23°C and 60% RH in August.

Further six day exposure

The six day exposure was a further subjection to rhizome extracts of the same samples from the three day experiment, thus the samples were exposed to the knotweed extracts for a total of nine days. The same 40 petri dishes were filled with sterile planting soil and each sample was replanted in its respective petri dish. The final masses from the three day experiment were the starting masses for the six day experiment. Samples were rehydrated by watering with 15 ml of designated extract for six days. Final dry mass was determined as previously described for the three day treatment.

Data analysis

Changes in green biomass were determined by calculating the percentage of remaining mass for each sample after 3 and 9 days of exposure. We arcsine transformed the biomass ratios to reduce deviations from normality for ANOVA. Graphs show raw data.

The null hypothesis of no difference among means by length of exposure and concentration of extract was tested with a factorial ANOVA (for the 3 day exposure) and a repeated measures factorial ANOVA (for the 9 day exposure) with $\alpha = 0.05$. Statistical and graphical analyses were performed with Excel 2010, Statistica ver. 11.0 and SYSTAT 12 for Windows.

Results

Preliminary dilution series

Mean seed germination ranged from 0 to 5 of 10 seeds (Table 1). Seed germination was affected starting at the 10% concentration, based on examination of dispersion around the means (Table 1). Thus, 10% was used as the lowest concentration of extract in the moss experiment.

Three-day exposure

In the first three days, all samples, including the controls, showed a decrease from initial to final mass (Fig. 1). Both moss species progressively decreased in green biomass as the concentration of extract increased (Fig. 1). For *Atrichum angustatum*, masses differed greatly among concentration levels. The final masses of the control samples were significantly higher than the final masses of the samples that were exposed to 25, 50 and 75% extract concentrations (Fig. 1). The control was not significantly different from the 10% group. With *Thuidium delicatulum*, the decrease in mass differed greatly between the control (0%) and each other concentration (10, 25, 50 or 75%) (Fig. 1). Thus, the effect of concentration on the final masses of these samples was highly significant ($F = 84.4$, $p < 0.001$). *Atrichum angustatum* and *T. delicatulum* reacted differently to the same concentrations. *A. angustatum* had a greater percentage of its biomass sur-

Table 1. Mean garden cress seed germination (of 10 seeds planted per group, n = 8 groups per concentration).

Concentration, %	Mean germination	SD	SE
0	4.0	2.5	0.9
1	4.3	2.0	0.7
3	5.1	2.0	0.7
5	4.8	2.3	0.8
10	4.3	1.2	0.4
25	2.1	1.9	0.7
50	1.4	1.8	0.7
75	0.5	0.5	0.2
100	0.0	0.0	0.0

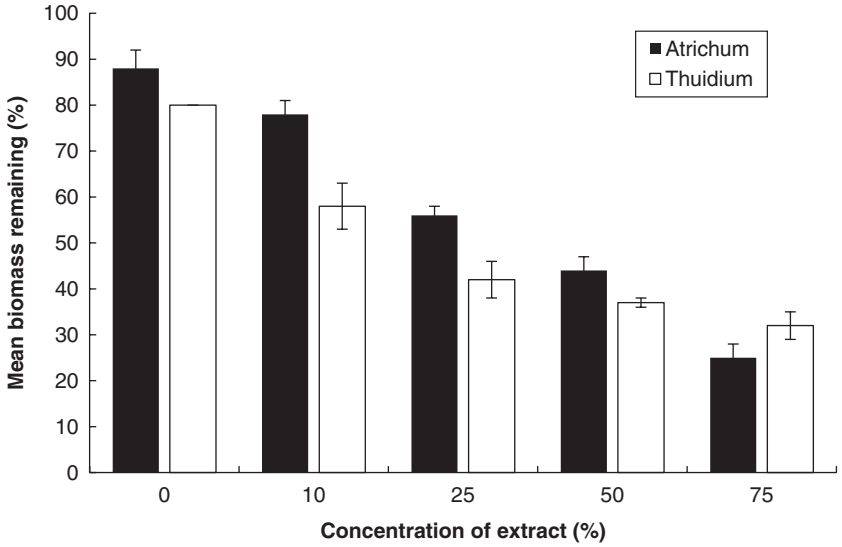

Figure 1. Biomass changes of two moss species under different knotweed extract concentrations after three days exposure. Bars represent mean per cent green biomass remaining, and error bars represent ± SE.

vive than *T. delicatulum* except at the 75% concentration (Fig. 1). *Atrichum angustatum* decreased further in mass at every concentration level while *T. delicatulum* had masses that were close in value at the 25, 50 and 75% level (Fig. 1). The effect of species on the final masses of these samples was highly significant ($F = 14.5$, $p = 0.001$). Finally, the interaction between species and concentration on the final mass of the samples was significant ($F = 4.3$, $p = 0.007$).

Further six-days exposure

After weighing, the surviving moss material from the three-days experiment was replanted and exposed to the same extracts for six more days. Again, starting with *A. angustatum*, all samples, including the control, continued to decrease in mass (Fig. 2). The remaining mass of each sample became smaller and smaller as concentration level increased (Fig. 2). After six days, 25, 50 and 75% concentrations had samples with less than a fifth of their starting mass remaining (Fig. 2).

Similarly for *T. delicatulum*, all samples, including the control, continued to decrease in mass as the concentration of extract increased (Fig. 3). Samples exposed to the 50% and 75% extracts retained means of only 3% green biomass remaining (from the mass at beginning of the experiment), equivalent to almost complete death of these samples (Fig. 3).

When comparing the green biomass changes over time, concentration had a highly significant effect on the final masses of the samples ($F = 136.3$, $p < 0.001$). The final masses differed significantly between species as well ($F = 12.4$, $p = 0.001$), and the interaction of concentration and species was weakly significant ($F = 3.5$, $p = 0.019$). The moss samples exposed to the same concentrations differed significantly in their final mass from the three day to the further six-days exposure ($F = 6.7$, $p = 0.001$). The interac-

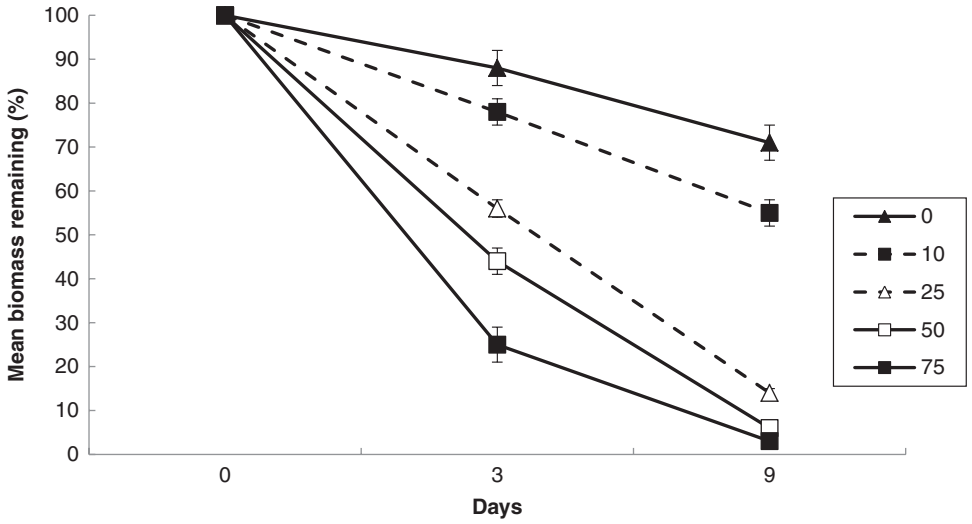

Figure 2. Changes in *Atrichum angustatum* green biomass after three and nine days exposure to 0, 10, 25, 50 and 75% concentrations of aqueous knotweed extracts. Points represent mean per cent green biomass remaining, and error bars represent ± SE.

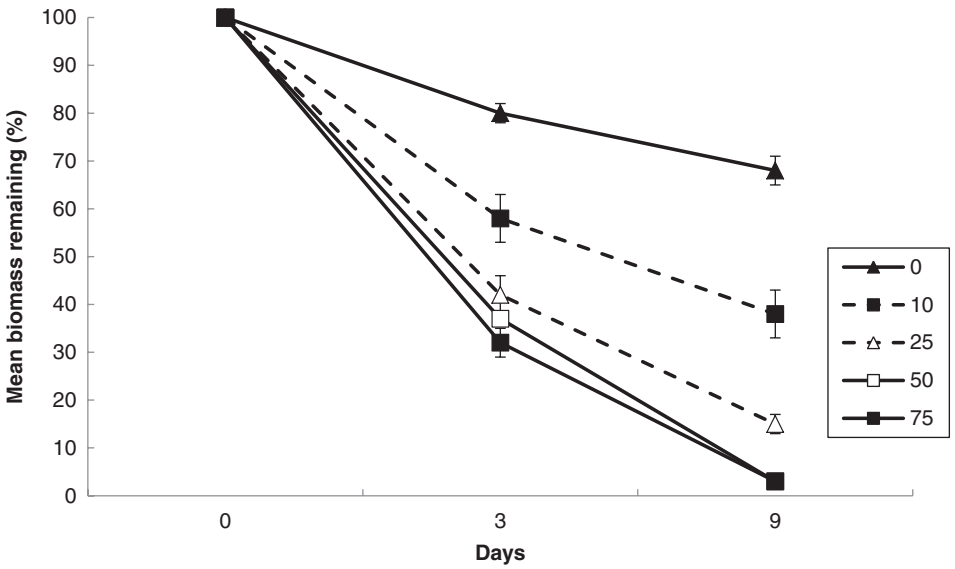

Figure 3. Changes in *Thuidium delicatulum* green biomass after three and nine days exposure to 0, 10, 25, 50 and 75% concentrations of aqueous knotweed extracts. Points represent mean per cent green biomass remaining, and error bars represent ± SE.

tion between species and exposure time was also significant ($F = 12.0$, $p = 0.002$). Finally, the interaction between species, concentration and exposure time had a weakly significant effect on the final mass of the samples ($F = 3.4$, $p = 0.02$).

Discussion

This study investigated the toxic effects of knotweed rhizome extracts on the growth of *Thuidium delicatulum* and *Atrichum angustatum* gametophytes. All samples, including the controls and those exposed to a graded series of extracts, experienced a decrease from their initial to final mass. The small loss of mass in the control samples was likely due to the stress of drying the moss samples repeatedly. Despite this, it is clear that the control samples decreased in mass little compared to the experimental groups, and the loss of green biomass in the moss material was proportional to the strength of the extract. Both *A. angustatum* and *T. delicatulum* showed trends of decreases in mass as the concentration of knotweed extract increased. *A. angustatum* was slightly more resistant to knotweed extracts than *T. delicatulum*, possibly due to the ability of *A. angustatum* to thrive in nutrient-poor soils. From the three-days exposure alone, a few conclusions can be drawn. First, we showed that knotweed extracts, at the concentration levels examined, were potent enough to cause both species to significantly decrease in mass after only three days of exposure. Additionally, after the further six-days exposure, both species continued to decrease in mass. At the 50% and 75% extract concentrations, the mosses retained a mean < 4% of their initial biomass, equivalent to almost complete death of these samples.

Clearly the knotweed extracts were toxic to the mosses. We expected this to be an effect of allelochemicals, inasmuch as knotweed is allelopathic to tracheophytes (Vrchotová and Šerá 2008, Murrell et al. 2011, Parepa et al. 2012). An alternate explanation is that solutes from the rhizomes or from decomposition of rhizome material had an osmotic effect on the mosses. However, since most mosses are drought tolerant and poikilohydric this seems unlikely (George Briggs, State Univ. of New York at Geneseo, pers. comm.).

We will assume that the toxicity we observed is due to allelochemicals, but we do not know how the laboratory results may translate to allelopathy in the field. The effects of knotweed on mosses may be modified by precipitation, flooding, soil organic matter or spatial separation between knotweed rhizomes and mosses. In urban areas, low humidity, air pollution and contaminants may stress mosses and have synergistic effects with allelochemicals. It is difficult to know what concentrations of knotweed allelochemicals are actually present and how long they persist in the soil or in knotweed crowns. However, because even the lowest concentration of extract (10%) reduced the green biomass of *A. angustatum* by 45% and *T. delicatulum* by 62% after only nine days of exposure, it is plausible that lower concentrations of extract over longer exposure times could produce the same negative effect in the field. The toxicity of aqueous rhizome extracts could explain scarcity of moss growth on live, but ready colonisation of dead, knotweed crowns by mosses observed in the field.

We found a pronounced effect of knotweed extracts on mature moss gametophytes. This accords with previous work that showed a negative effect of knotweed allelochemicals on the growth of mature tracheophytes (Parepa et al. 2012, Dommanget et al. 2014). That knotweed has been shown to chemically interfere with mature tracheophytes and now mosses is noteworthy. Water extracts of the aboveground parts of knotweed, as well as the rhizomes, were toxic to seedlings of tracheophytes in the laboratory (Vrchotová and Šerá 2008), and Murrell et al. (2011) found inhibitory effects of Bohemian knotweed on four species of European forbs in a greenhouse experiment. Inoue et al. (1992) identified two anthraquinones, emodin and physcion, from acetone extracts of giant knotweed, and both compounds inhibited lettuce seedlings. Jug et al. (2021) identified specific anhraquinones, flavanols, proanthocyanidins, stilbenes and other compounds in knotweed rhizome bark. These studies indi-

cate that allelopathy could be an important mechanism in knotweed's ability to invade and dominate plant communities. It seems unlikely that mosses would often exert an important competitive effect on knotweed in the northeast, thus we suggest that any inhibitory effects of knotweed on mosses are an incidental result of allelopathy that evolved to reduce competition from other tracheophytes or inhibit pathogens or herbivores. Nonetheless, knotweed suppression of moss growth could have a significant effect on the moss assemblages of habitats colonised by knotweed, and our experiment helps to explain the paucity of mosses attached to live knotweed crowns and beneath knotweed stands observed in urban and rural habitats of eastern New York and northeastern New Jersey.

It is well known that allelopathic effects of one tracheophyte on another in the laboratory do not necessarily translate into allelopathy in the field (Macías et al. 2004). Potential allelopathy can be modulated by soil and water conditions. A possible example is lush moss growth attached to knotweed stem bases and crowns on Vashon Island near Seattle, Washington State (Kiviat unpubl.), where precipitation or fog occurs on many more days of the year than in the northeastern states. Therefore, the interactions of knotweed and mosses should be investigated in the field under a variety of conditions, using knotweed stems and leaves as well as rhizomes. The specific compounds responsible for the observed inhibitory effects should be identified, and their concentrations measured in litter and soils beneath knotweed stands in regions subject to different conditions of precipitation, temperature and soil (e.g. Catskill Mountains, New York, versus the northwest coast of the US). Finally, a study investigating the effect of knotweed allelochemicals on moss spore germination and protonemal development would be informative.

Conclusions

We found a pronounced, negative effect of unidentified knotweed chemicals on mature gametophytes of the mosses *Atrichum angustatum* and *Thuidium delicatulum* related to increasing exposure times. This is the first study to document toxic effects of knotweed on bryophytes, the results of which lend support to the hypothesis that allelopathy is a mechanism in the effects of knotweed on other plants. Janice Glime (pers. comm.) has suggested that the toxic effect of knotweed rhizome extract on mosses might find application as a 'bryocide' in control of pest mosses on artificial substrates such as roofs and patios. However, managers of wild vegetation may find that reducing knotweed biomass may facilitate development of the moss stratum with its inherent biotic diversity. As of 2020, a classical biological control program using a sap-sucking insect against knotweed is being implemented in the US (NYISRI 2020); we recommend that knotweed stands where the insect becomes established be monitored for development of the bryoflora.

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