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Abstract Bohemian knotweed (*Polygonum* × *bohemicum*), the hybrid between Japanese and giant knotweed, is the most common invasive knotweed species in western North America and the most difficult to control. Invasive knotweed congeners spread aggressively along streams and establish dense monotypic stands, reducing riparian plant species diversity. Allochthonous organic matter inputs from riparian plants are an important source of energy and nutrients for organisms in small streams. However, little information exists concerning the influence of knotweed on stream processes. This study examines the quality of Bohemian knotweed leaves compared to native red alder and black cottonwood leaves, along with leaf-associated fungal biomass accumulation, macroinvertebrate communities, and decay rates from three forested streams in western Washington State. Senesced knotweed leaves were lower in nitrogen and phosphorus, and higher in cellulose, fiber, and lignin content than alder leaves, but were more similar to cottonwood leaves. Fungal biomass differed among species and changed over time. Macroinvertebrate shredders collected from leaf packs after 31 days were proportionately more abundant on alder leaves than knotweed and cottonwood. Decay rates were not significantly different among leaf species, but during the first 31 days alder broke down faster than knotweed. After 56 days, all of the leaf packs were mostly decomposed. Overall, these findings do not show major discrepancies between leaf species except those related to initial litter structural and chemical quality. However, changes in the timing and quantity of litter inputs are also important factors to be considered in understanding the impact of invasive knotweed on stream ecosystem processes.

Keywords Bohemian knotweed · Japanese knotweed · *Polygonum* · *Fallopia* · Freshwater · Exotic

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Introduction

Organic matter inputs from riparian vegetation provide crucial sources of energy for aquatic ecosystems (Benfield 1997; Wallace et al. 1997; Webster and

Benfield 1986) and the diversity and density of riparian plants can fundamentally affect the nutritional quality, quantity, and timing of allochthonous inputs to streams (Benfield 1997; Graça 2001; Kominoski et al. 2011; LeRoy and Marks 2006). Decomposition rates of different leaf litter species are often influenced by litter quality, particularly the carbon:nitrogen (C:N) ratio and lignin content (Hladyz et al. 2009; Irons et al. 1988; Schindler and Gessner 2009). Nitrogen (N) often enhances the nutritional quality of leaf litter and may accelerate litter decomposition by increasing the colonization and growth of aquatic fungi and its consumption by detrital consumers (i.e., shredders). In contrast, lignin and cellulose reduce the nutritional quality of leaf litter and may slow litter decomposition by resisting physical breakdown, increasing leaf toughness, and inhibiting microbial activity. Secondary plant compounds, such as condensed tannins, may also influence decomposition and leaf litter palatability (Hagerman and Butler 1991; Irons et al. 1988). Changes in riparian plant composition have the ability to alter aquatic food webs if leaf litter inputs differ in their intrinsic properties, regardless of the geographical origin of the leaves (Cohen et al. 2012; Graça 2001; Parkyn and Winterbourn 1997). In particular, novel sources of leaf litter due to non-native species invasions may result in dramatically altered nutrient content and thus stoichiometry of leaf litter inputs to streams (Hladyz et al. 2009), thereby having profound impacts on consumers within these detritus-based systems. Here we discuss a recent and overwhelming invasion by a riparian species that may be influencing the structural and functional processes of stream ecosystems.

Invasive knotweed species: Japanese (*Polygonum cuspidatum* Sieb. & Zucc., syn. *Fallopia japonica*), giant (*P. sachalinense* F. Schmidt ex Maxim.), and their hybrid, Bohemian (*P.* × *bohemicum* Chrtek and Chrtková), are rhizomatous herbaceous perennial plants native to eastern Asia that were introduced to Europe and North America in the 1800s as ornamental and fodder plants (Barney et al. 2006). Today, these species are considered among the most serious exotic weeds in Europe and North America, particularly along stream and riparian corridors. During the spring growing season, knotweed plants emerge from belowground rhizomes forming robust erect stems 3–4.5 m tall (depending on the species) with large ovate leaves, which abscise from the stems following senescence in late fall. The rhizome system of knotweed is quite extensive and can effectively propagate through the fragmentation and downstream dispersal of rhizomes or stem fragments. Once established, knotweed typically forms a dense thicket that shades and successfully out-competes other riparian vegetation (Gerber et al. 2008; Urgenson et al. 2009).

By displacing native riparian plant assemblages, knotweed stands can potentially disrupt or alter the input and flow of terrestrial organic matter in streams. For example, in riparian areas invaded by giant knotweed, the input of leaf litter from native species was reduced by 70 % (Urgenson et al. 2009). In addition, the translocation and resorption of foliar N during leaf senescence was 76 % in giant knotweed, but only 5 % in N-fixing red alder (*Alnus rubra* Bong.) and 33 % in willow (*Salix* species), resulting in higher C:N contents in senesced leaves of giant knotweed (52:1) compared to red alder (21:1) or willow (32:1) (Urgenson et al. 2009). Similarly, prior studies have reported that Japanese knotweed leaves have C:N ratios ranging from 21:1 to 48:1 and lignin content of 9.1–13.7 % (Bottollier-Curtet et al. 2011; Lecerf et al. 2007). Therefore, the leaf litter of invasive knotweed congeners is considered low quality and should decompose slower than leaves of higher quality (Webster and Benfield 1986).

Prior research comparing in-stream knotweed and native litter decomposition and associated biota has been spatially and taxonomically limited, with results being quite variable among the study sites examined. For example, Lecerf et al. (2007) compared litter decomposition rates, fungal biomass, and invertebrate assemblages between invasive Japanese knotweed and native English oak (*Quercus robur* L.) within an invaded and an un-invaded stream in England (Pennines) and again in France (Pyrenees). In both regions, Japanese knotweed leaves had slightly higher N and lower lignin content than oak leaves. Yet, they observed no difference in decomposition rates or invertebrate community structure between litter species or streams in England. In France, litter breakdown and the relative abundance of large invertebrate shredders were enhanced for both knotweed and oak leaves within the invaded stream. Fungal biomass (as measured by ergosterol content) was higher on knotweed in England and higher on oak in France, but neither difference correlated with observed decomposition rates. Another study in southwestern

France, observed no difference in litter decomposition or aquatic invertebrate assemblages between Japanese knotweed and native European dewberry (*Rubus caesius* L.), even though the native plant was of higher quality (lower C:N, C:P, and lignin content) than knotweed (Bottollier-Curtet et al. 2011). In Idaho, USA, litter decomposition and invertebrate compositions were also similar among invasive Japanese knotweed, native black cottonwood (*Populus trichocarpa* Torr. and Gray) and gray alder (*Alnus incana* L.), even though the knotweed and cottonwood leaves had less than half the N and phosphorus (P) compared to alder leaves (Braatne et al. 2007). Currently, no study has addressed the invasive hybrid Bohemian knotweed that is aggressively invading riparian stream corridors in North America.

Invasive knotweeds are increasingly naturalized in heavily infested areas due to their aggressive growth, extensive rhizome system, and efficient vegetative propagation; all of which makes eradication very difficult (Bashtanova et al. 2009; McHugh 2006). In view of this rapid expansion, more studies are needed to understand the ecological effects of invasive knotweed species on stream dynamics and higher trophic levels. This is particularly urgent as increases in temperature and atmospheric CO_2 predicted by global change scenarios are expected to expand the geographic range of invasive knotweeds (Beerling and Woodward 1994). In North America, Bohemian knotweed is the most common species, whereas Japanese knotweed is predominant in Europe (Gaskin et al. in review; Zika and Jacobson 2003). Of the invasive knotweed taxa, Bohemian is the most successful in terms of regeneration and establishment of new shoots (Bímová et al. 2003; Pysek et al. 2003), the most difficult to control (Bímová et al. 2001), and the most genotypically diverse (Gaskin et al. in review; Pysek et al. 2003). In this study we examined the differences in litter quality, decomposition rates, aquatic fungal colonization, and benthic macroinvertebrate communities among invasive Bohemian knotweed, native red alder and black cottonwood leaf litter. Litter decomposition was replicated in three streams in western Washington State (USA). Overall, we hypothesized that (1) knotweed leaf litter would differ from the native litter species in terms of nutrient and structural content, (2) these differences in litter quality would lead to differential colonization and growth of aquatic fungi (as measured by total fungal biomass) and its consumption by aquatic invertebrates, and (3) these combined differences in litter traits, microbial colonization and growth, and invertebrate detritivore activity would result in differential mass loss for native compared to exotic litter species.

Methods

Study sites

Field experiments were conducted in three streams located in the Chehalis River basin of western Washington State (Fig. 1), which is characterized by a temperate, maritime climate [mean annual temperatures range from 5 to 17 °C and mean annual precipitation is around 170 cm (WRCC 2013)]. The streams were 2nd to 3rd order, forested, and low gradient (<5 %). Porter Creek was the largest with a drainage area of 86.6 km^2 and bankfull width of 17.4 m during the experiment, followed by Wildcat Creek (55.0 km^2 area, 13.7 m bankfull), and Stony Creek (7.8 km^2 area, 5.9 m bankfull). In each stream, a 25 m long study reach was established for securing leaf packs and repeat site visits. The study reaches had similar channel characteristics (pool-riffle sequences with gravel-cobble substrate) and ranged in elevation from 27.1 to 61.7 m (Wildcat < Porter < Stony). The surrounding land use was primarily rural housing and small-scale agriculture. Because these streams support spawning salmon populations, they were buffered by riparian zones that prohibit development and timber harvest. Riparian areas along the study streams were invaded by Bohemian knotweed (<50 % cover), although herbicide-based control activities were in the process of reducing knotweed cover. Western redcedar (*Thuja plicata* Donn), red alder and black cottonwood were the primary riparian tree species present, but recruitment of all of these species was significantly reduced in the presence of knotweed invasion.

Field experiment

Freshly senesced leaves of red alder, black cottonwood, and Bohemian knotweed were collected during October and November 2010. Senesced leaves were collected from at least four different locations per species in the Chehalis Basin to better encompass

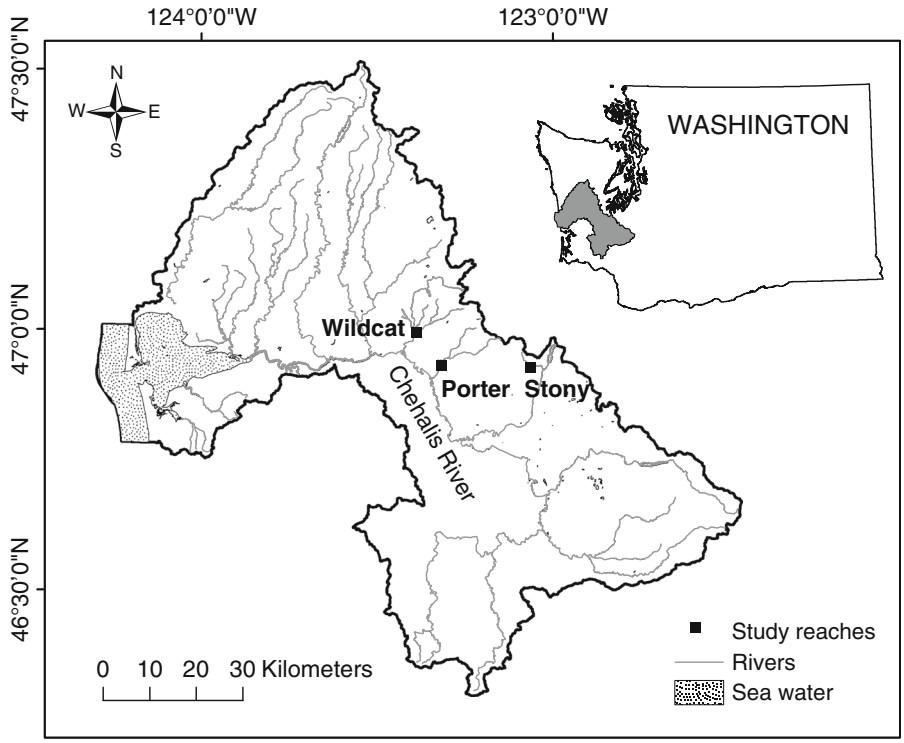

Fig. 1 Location of study reaches along Porter Creek, Stony Creek, and Wildcat Creek in the Chehalis River Basin of southwest Washington State, USA

within-species genetic diversity (LeRoy et al. 2007). The leaves were air-dried and weighed into packs of 5.00 ± 0.20 g per species. Single species leaf packs were enclosed in large mesh bags (bag size 30 × 20 cm, mesh size 1 × 1.5 cm) to allow access by aquatic insects. A total of 225 leaf packs were distributed among the three streams in January 2011. Leaf packs were transported in individual paper sacks so that dry leaf fragments broken during transport and handling were weighed and recorded as a correction for handling loss.

At the stream site, the packs were randomly distributed and secured to heavy metal T-bar fence posts that were anchored to the bottom of the streambed with rocks. Subsets of 5 packs per species per stream were removed after 0, 15, 31, and 56 days. The study was intended to conclude after 12 weeks; however, most of the leaf litter had decomposed by week 8. As a consequence, all remaining packs (8–10 packs per species per stream) were removed on day 56. Stream flows for most of the study period, January through March 2011, were stable and typical of winter-time base flows. However, 1 week into the study on January 16th a large rain event caused above bankfull flows at all of the streams, lasting 24 h or less. Several leaf pack replicates were lost at this time, but this loss did not overly influence the results of the study.

Water parameters

Water temperature (°C) at each stream was recorded hourly throughout the experiment (January–March 2011) with HOBO Pro v2 U22 data loggers (Onset Computer Corporation Inc., Pocasset, MA, USA). Stream water pH, conductivity (temperature compensated, μS/cm), and dissolved oxygen (DO, mg/L) were measured in the field during the experiment setup and subsequent harvest dates (YSI Inc., Yellow Springs, OH). Water samples for nutrient analyses were collected from each stream on the same dates. Water was filtered in the field through glass fiber filters (Whatman GF/C), transported to the laboratory on ice and frozen until analysis. Nutrients were analyzed using a SEAL AA3 Flow-Injection Nutrient Analyzer (SEAL Analytical Inc., Mequon, WI, USA) following

established standard protocols from the manufacturer (SEAL 2013). Phosphorous concentrations (SRP) were analyzed using the ascorbic acid/molybdate method (method G297-03). Nitrite-Nitrate concentrations were analyzed using the sulfanilamide method (method G172-96), following reduction by an in-line copper-cadmium reductor column. Ammonium concentrations were analyzed using the Berthelot reaction (Salicylate) (method G171-96).

Leaf litter parameters

Structural leaf litter properties such as acid detergent fiber, cellulose, and lignin were measured on initial litter packs using a gravimetric method proposed by Goering and Van Soest (1970) and modified by Gessner (2005b). Crucibles and filters were pre-fired in a muffle furnace (Lindberg/Blue M, Asheville, NC) at 550 °C for 1 h. Ground leaf litter subsamples (250 mg) were digested in acid detergent at 100 °C for 1 h. Acid detergent cellulose (ADC), was determined by weight following a cool (15 °C) sulfuric acid (72 % H_2SO_4) digestion for 3 h and washing and oven-drying the remaining residue. Finally, sample residues were placed in a muffle furnace and combusted at 550 °C for 3 h to determine acid-detergent lignin (ADL) content. Values for ADC and ADL were converted to percentages based on the initial dry weight of each sample.

Leaf properties of C:N, C:P, fungal biomass, and ash-free-dry-mass (AFDM) were measured on initial litter samples and harvest dates (0, 15, 31, and 56 days). Upon removal from the streams, leaf packs were placed into individual plastic bags in a cooler and immediately transported to the lab. There the leaves were rinsed to remove any silt and insects, and 10 discs (10 mm dia.) were cut from remaining leaf material of each leaf pack to estimate fungal biomass, as measured by ergosterol concentration. Discs were stored frozen (−20 °C) in the dark prior to analysis. Frozen leaf disks were lyophilized to dryness, weighed, and ergosterol extracted and partially purified by solid-phase extraction (Gessner 2005a). Ergosterol in samples was separated and quantified by a Shimadzu High Pressure Liquid Chromatography (HPLC) system (Shimadzu Scientific Inc., Columbia, Md USA) using a LichroSpher 100 RP-18 column (0.46 × 25 cm, mobile phase HPLC grade methanol, flow rate of 1.5 mL/min). Ergosterol was detected at 282 nm and identified and quantified based on comparison with ergosterol standards (Fluka Chemical). A 5.5 mg/g conversion factor was used to convert ergosterol (μg/g) into fungal biomass (mg/g) (Gessner and Chauvet 1993). The dry masses of the discs cut from each leaf pack were measured and included in the remaining dry mass for each leaf pack. The remaining litter was dried at 50 °C for 48 h, weighed to the nearest 0.01 g, and then ground to powder. A subsample of ground material from each leaf pack was analyzed for % C, N, and P to determine C:N and C:P ratios. Plant litter C and N concentrations were determined using a Costech ECS 4010 elemental analyzer (Costech Analytical Technologies Inc., Valencia, Ca). Phosphorus concentrations were determined as above using a SEAL AA3 Flow-Injection Nutrient Analyzer (molybdate-ascorbic acid method) following combustion (500 °C) and hot HCl extraction of ground litter subsamples. Additional subsamples of ground plant material were weighed, ashed at 550 °C for 4 h, and reweighed to determine litter AFDM remaining.

Leaf litter decomposition was compared for both mass lost at each harvest date and overall decay rate per species per stream. Decay rates (k/day) were calculated by linear regression of ln-transformed AFDM (negative exponential model $M_t = M_o \times e^{-kt}$, where M_o is the initial mass, M_t is the remaining mass at time t and k is the decay rate) with a free intercept. To account for small, but potentially important, differences in temperature between streams, decay rates in degree days^{-1} were also calculated per species per stream by replacing time (t) in the above formula by the sum of mean daily temperatures accumulated for each harvest day.

Aquatic macroinvertebrate communities on the leaf packs were collected from the day 31 packs by running the leaf litter rinsing water through 500 μm mesh and preserving all remaining material in 80 % ethyl alcohol. Aquatic macroinvertebrates were counted and identified to the lowest reliable taxonomic level (generally genus), except for Chironomidae, which were identified to sub-family or tribe. All macroinvertebrates were assigned a functional feeding group (FFG) category (Merritt et al. 2008).

Statistical analyses

Leaf packs were deployed to streams in a randomized complete block design. We evaluated the effects of

species, harvest day, and their interaction on leaf pack properties of C:N, C:P, fungal biomass, and AFDM remaining using mixed-effects ANOVA, with stream as a random effect and harvest day (0, 15, 31, and 56 days) as a repeated measure (SAS v.9.3 Proc Mixed). To determine the covariance structure over time, we tested 5 common covariance structures that do not require equal time spacing and chose the one with the best fit using Akaike's information criterion corrected for small sample sizes for each response (compound symmetry for C:N, C:P, and fungal biomass, spatial power for AFDM) (Wolfinger 1993). We evaluated the effect of species on leaf properties collected at one point in time [fiber, cellulose, and lignin (day 0); aquatic invertebrate abundances, taxa richness, and FFG proportions (day 31)] or representative of the entire time period as a whole (decay rates, k) using mixed-effects ANOVA, but with no repeated measures. The proportion of AFDM remaining per leaf pack at day 31 was added as a covariate to the invertebrate analyses in order to standardize the invertebrate counts by available leaf mass. We checked all final model residuals for deviances from the normal distribution, but only AFDM and fungal biomass needed to be $\log_e$ transformed prior to statistical analyses. Significant mean differences between species or harvest day effects were determined using the Tukey–Kramer adjustment for pairwise comparisons (overall $\alpha = 0.05$). For properties measured over time, significant mean differences among species within each harvest day (we tested across species within each date, but not across dates within species) were determined with a Bonferroni correction for 12 tests ($\alpha = 0.0042$).

Multivariate analyses of macroinvertebrate taxa abundances were used to describe stream and species patterns among leaf packs. Nonmetric multidimensional scaling (NMS) ordinated 45 leaf packs against 43 taxa and correlated community and physical variables with axes in the ordinations (PC-ORD v.6.04). Taxa abundances were $\log_{10}(x + 1)$ transformed and relativized by the taxa maximum. Rare taxa that were observed in only one out of 45 samples were removed (7 rare taxa). Sørenson (i.e., Bray–Curtis) distance measured dissimilarity. The ordination was performed with 250 runs with the data and the run with the lowest stress (16.74) and a stability criterion of 0.00001 was selected for analysis. The final solution was 2-dimensional, representing 82 % of the total variance. Joint plots (line vectors) were used to display the strongest correlations (Pearson's $r > 0.5$) of leaf pack quantitative measures at day 31 (total abundance, taxa richness, functional feeding groups, mass remaining, fungal biomass, C:N and C:P) along the ordination axes. Each quantitative variable is tested for correlation with the ordination axes separately; therefore correlation among the variables does not affect the results. Two-way Permutative Multivariate Analysis of Variance (PerMANOVA in PC-ORD) was used to compare macroinvertebrate community structure among streams, leaf species, and their interaction.

Results

Stream water

Water parameters measured over the course of the experiment from the three streams show the reaches to be similar to each other (Table 1). From January through March 2011 water temperatures varied from 0.5 to 9.3 °C, with Porter Creek typically cooler than Stony and Wildcat Creeks, but the streams never differed by more than 1.3 °C at any one time. The streams were all generally pH neutral, low in conductivity and high in dissolved oxygen. All of the streams had dissolved chemical levels typical of undisturbed, forested streams in the Pacific Northwest, U.S.A. (Compton et al. 2003).

Leaf structure and nutrients

Freshly senesced leaves of the three species differed significantly in terms of their fiber, cellulose, and lignin proportions (Fig. 2). Knotweed contained significantly more fiber and cellulose than alder and cottonwood ($p \leq 0.0028$ for all); and more lignin than alder ($p = 0.0033$). During the experiment, the alder leaves appeared brittle, while the knotweed leaves felt pliable, likely due to their higher relative fiber, cellulose, and lignin contents. Although the leaf packs were handled in the same manner, the mean % leaf mass lost due to initial handling alone (measured leaf fragments to correct day-0 leaf-pack dry mass) was small, but mass loss was greatest for alder leaves (0.42 %), followed by cottonwood (0.26 %), and lowest for knotweed (0.05 %).

Table 1 Physio-chemical characteristics, mean (min–max), of the study streams during the decomposition experiment

Parameter	Stony Crk.	Wildcat Crk.	Porter Crk.
Temperature (°C)	6.4 (1.8–8.9)	6.5 (1.8–9.3)	6.0 (0.5–8.4)
pH	7.0 (6.8–7.2)	6.9 (6.7–7.2)	7.3 (7.1–7.6)
Conductivity (μS/cm)	43.5 (39.8–47.5)	62.7 (57.5–66.6)	45.9 (43.6–48)
Dissolved oxygen (mg/L)	12.4 (12–13.1)	12.1 (11.7–12.4)	12.8 (12.4–13.1)
NO_3/NO_2–N (μg/L)	579 (524–677)	627 (574–698)	638 (617–667)
NH_4–N (μg/L)	33 (24–49)	11 (5–17)	11 (4–17)
PO_4–P (μg/L)	11 (8–15)	15 (10–18)	10 (9–13)

Water temperature was recorded hourly throughout the study period. All other measurements were recorded during the daytime at day 0, 15, 31, and 56 (January–March 2011)

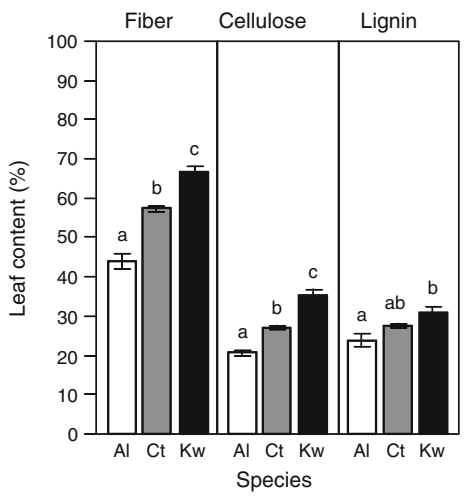

Fig. 2 Fiber, cellulose, and lignin proportions (mean ± 1 SE) from senesced leaves of red alder ("Al", *white bars*), black cottonwood ("Ct", *grey bars*), and Bohemian knotweed ("Kw", *black bars*) at the start of the experiment (day 0). *Letters* denote significant pairwise comparisons among species (Tukey–Kramer adjusted $p < 0.05$)

The leaf species also had significantly different C:N and C:P ratios that changed over time (Fig. 3). Prior to decomposition, at day 0, alder leaves had significantly lower C:N and C:P ratios than knotweed and cottonwood ($p \leq 0.0019$ for all), while knotweed was significantly lower than cottonwood for C:N ($p < 0.0001$), but not C:P ($p = 0.3713$). The proportion of N in decaying leaf litter increased during decomposition, likely due to increased microbial immobilization, resulting in a decrease in C:N ratios for all three species (Fig. 3a). After 31 days, only alder had significantly lower C:N than cottonwood or knotweed ($p < 0.0001$ for both). Phosphorus was slower to immobilize on the leaf surfaces as C:P ratios actually increased for the first 15 days, but then decreased after 31 days to below pre-decomposition levels in all the species with no significant differences among species (Fig. 3b).

Decomposition

Decay rates, k (day^{-1}) (mean ± SE), were similar among knotweed (0.0269 ± 0.0024), alder (0.0272 ± 0.0024), and cottonwood (0.0283 ± 0.0019) ($p = 0.4484$). Decay rates are given for each species from each stream in Table 2. Temperature corrected decay rates (degree $days^{-1}$) were also similar among species ($p = 0.4349$). Since k integrates differences in mass loss throughout the entire study, looking more closely at patterns in mass loss at each harvest date might reveal different results. Comparisons of leaf pack mass remaining (%) among species at each harvest day do indicate some significant differences in decomposition (Fig. 3c). For example, after only 15 days, alder lost significantly more mass than knotweed and cottonwood ($p < 0.0001$ and $p = 0.0013$, respectively). After 31 days, alder had still lost the most mass, but the difference was only significant compared to knotweed ($p = 0.0017$). After 56 days, all three species were mostly decomposed (90–95 %) and not significantly different from one another in mass loss ($p \geq 0.3726$).

Fungal biomass

Fungal biomass differed significantly among species and changed over time (Fig. 3d). Early differences among the species were due to higher levels of fungal biomass on senesced knotweed leaves prior to aquatic

decomposition (day 0) compared to alder and cottonwood ($p < 0.0001$ for both). After 15 days of decomposition, fungal biomass increased on all the leaf species, but knotweed still had significantly more fungal biomass than alder ($p < 0.0001$) and alder had significantly more fungal biomass than cottonwood ($p < 0.0001$). After 31 days, alder and cottonwood developed substantial fungal biomass such that mean values for all three species were no longer significantly different ($p \geq 0.1849$). After 56 days, fungal biomass dropped on alder and even more so on knotweed, but continued to rise on cottonwood, which showed significantly greater fungal biomass than knotweed at this final harvest date ($p = 0.0025$).

Table 2 Decay rates (k/day) of red alder, black cottonwood, and Bohemian knotweed leaves submerged for 56 days in the study streams

Species	Stream	k/day (1 SE)	Adj. R^2
Alder	Porter	0.0282 (0.0025)	0.844
	Stony	0.0254 (0.0025)	0.808
	Wildcat	0.0279 (0.0021)	0.871
Cottonwood	Porter	0.0309 (0.0017)	0.932
	Stony	0.0274 (0.0021)	0.855
	Wildcat	0.0266 (0.0020)	0.873
Knotweed	Porter	0.0277 (0.0023)	0.865
	Stony	0.0270 (0.0021)	0.846
	Wildcat	0.0261 (0.0027)	0.805

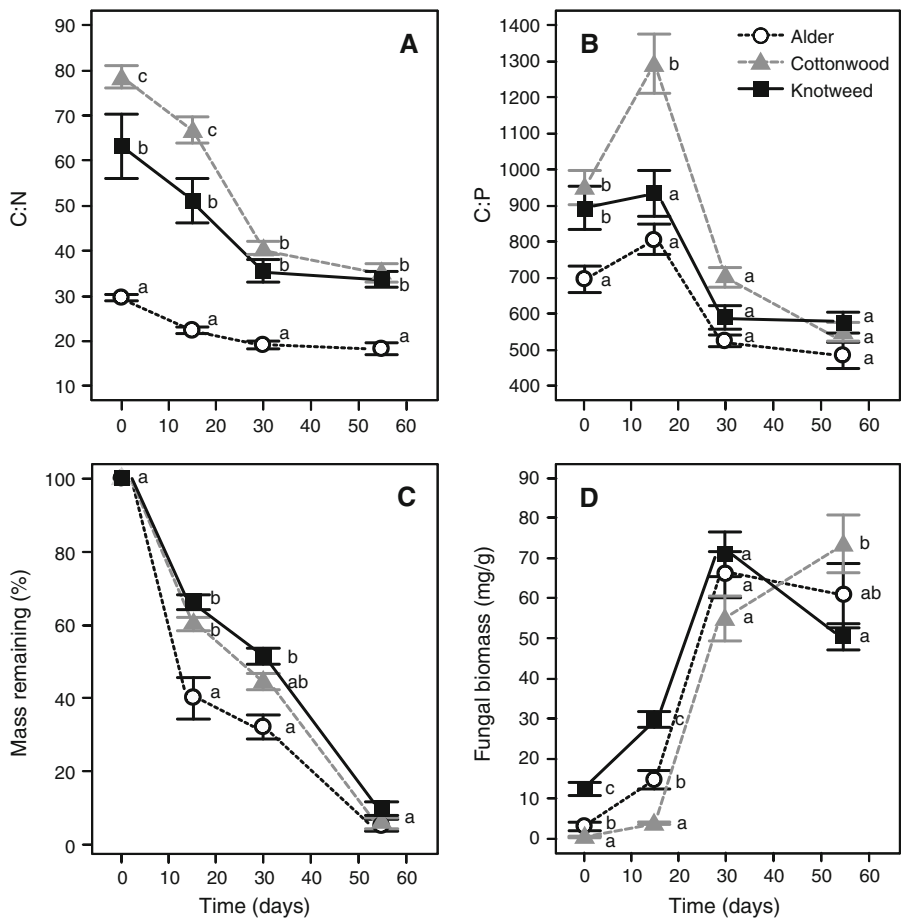

Fig. 3 Carbon:Nitrogen (**a**), Carbon:Phosphorus (**b**), proportion of mass remaining (**c**), and fungal biomass (**d**) from leaf packs of red alder (*white circles*), black cottonwood (*grey triangles*), or Bohemian knotweed (*black squares*) during decomposition (mean ± 1 SE). Fungal biomass values were ln-transformed for statistical analysis. *Letters* denote significant difference among species at each harvest date (Bonferroni correction for 12 pairwise comparisons, $p < 0.0042$)

Aquatic macroinvertebrates

Macroinvertebrate total abundance and taxa richness per leaf pack after 31 days (Table 3) were not significantly different among leaf species ($p = 0.3380$ and $p = 0.4278$, respectively). However, the proportion of shredding invertebrates (primarily *Zapada* sp., *Malenka* sp., and *Capnia* sp.) was significantly higher on alder than knotweed or cottonwood leaves ($p = 0.0160$). The number of shredder taxa was also higher on alder leaves, although species differences were not significant ($p = 0.0858$). Collector-gathering invertebrates (primarily Chironomidae sp., *Ephemerella* sp., and *Paraleptophlebia* sp.) were most abundant (Table 3), but showed no differences among species ($p = 0.6421$). Scrapers (e.g., *Cinygmula* sp., *Epeorus* sp., and *Taenionema* sp.), collector-filterers (e.g., Simuliidae sp.), and predators (e.g., *Hesperoperla pacifica* and *Isoperla* sp.) were low in abundance and not significantly different among leaf species ($p = 0.0795$, $p = 0.2280$, and $p = 0.3782$, respectively).

Macroinvertebrate community composition from the leaf packs harvested after 31 days was foremost influenced by stream ($F_{(2,36)} = 16.77$, $p = 0.0002$), with weaker, but significant differences among leaf species ($F_{(2,36)} = 1.88$, $p = 0.0322$), and no significant stream by species interaction ($F_{(4,36)} = 1.32$, $p = 0.1270$) (Fig. 4). Pairwise comparisons reveal that knotweed leaf packs hosted significantly different macroinvertebrate communities than either alder or cottonwood, but that there were no significant differences between the native species. In particular, knotweed leaf packs within Stony Creek had greater abundance, taxa richness, % scrapers, and % predators than the alder and cottonwood leaf packs. In reverse, knotweed leaf packs within Wildcat Creek had lower abundance and taxa richness, but similarly greater % predators compared to the alder and cottonwood leaf packs. Overall, mean abundance and taxa richness was highest at Porter Creek (267 individuals, 20 taxa), followed by Stony Creek (128 individuals, 18 taxa), and then Wildcat Creek (49 individuals, 10 taxa). On average, collector-filtering and scraping invertebrates were proportionately greater at Porter Creek (15 and 8 %, respectively), collector-gatherers were greater at Stony Creek (76 %), and shredders were greater at Wildcat Creek (22 %). Leaf pack measures of mass remaining (%), fungal biomass (mg/g), C:N and C:P at day 31 were not correlated with the NMS ordination (Pearson's $r < 0.5$).

Table 3 Mixed-effects ANCOVA estimates of aquatic invertebrate abundance, taxa richness, and functional feeding group proportions (mean ± 1 SE)

Response	Alder	Cottonwood	Knotweed
Abundance (#)	74.4 (75.8)[a]	128.3 (56.2)[a]	240.8 (71.9)[a]
Taxa richness (#)	17.4 (3.4)[a]	15.0 (3.2)[a]	14.8 (3.3)[a]
Shredder (%)	**21.7 (2.7)[a]**	**11.0 (2.5)[b]**	**10.7 (2.7)[b]**
Scraper (%)	2.6 (2.0)[a]	3.2 (1.9)[a]	5.9 (2.0)[a]
Collector-filter (%)	8.7 (5.6)[a]	6.6 (5.1)[a]	1.1 (5.5)[a]
Collector-gather (%)	66.7 (6.5)[a]	73.1 (4.8)[a]	72.5 (6.2)[a]
Predator (%)	2.7 (1.3)[a]	4.1 (1.3)[a]	6.3 (1.3)[a]

Invertebrates were collected from red alder, black cottonwood, and Bohemian knotweed leaves after 31 days of decomposition. Letters denote significant pairwise comparisons among species (Tukey–Kramer adjusted $p < 0.05$) and significantly different values are in bold

Discussion

The potential influences of riparian invasion by knotweed on stream ecosystems are complex, with alterations to the riparian forest by knotweed

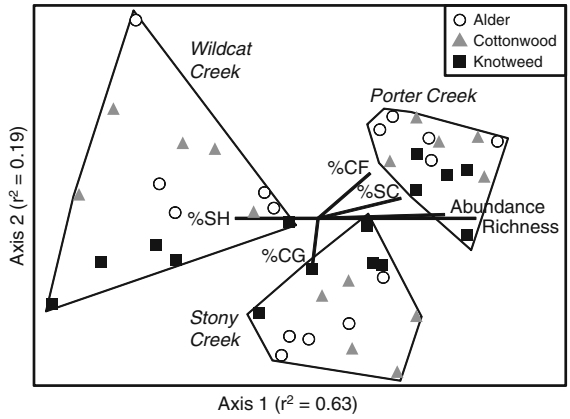

Fig. 4 Two-dimensional NMS ordination of aquatic insect communities (43 taxa) collected from the leaf packs (n = 45). Sample points denote a single leaf pack of red alder (*white circles*), black cottonwood (*grey triangles*), or Bohemian knotweed (*black squares*). Joint plots (*line vectors*) display the strongest correlations (Pearson's $r \geq 0.5$) between quantitative variables along the ordination axes. Correlated functional feeding group proportions are scraping (SC %), shredding (SH %), collector-filtering (CF %), and collector-gathering (CG %) macroinvertebrates

congeners being both dramatic and widespread. Although other studies have addressed the larger-scale influence of knotweed invasion on native tree and understory regeneration (Gerber et al. 2008; Urgenson et al. 2009; Urgenson et al. 2012), the present study addressed differences in litter quality and decomposition rates between knotweed and native tree species. The considerable differences in litter quality and leaf structure led to differences in microbial colonization and growth by aquatic fungi, shredding invertebrate proportions, and mass loss at intermediate decay stages.

Leaf litter quality was significantly different prior to the start of the experiment and maintained strong differences throughout the decomposition process. In particular, the Bohemian knotweed litter was consistently more pliable, composed of more structural carbon compounds (i.e., fiber, cellulose, and lignin; FCL), and generally showed intermediate C:N and C:P. The more stable leaf substrate and moderate nutrient content of knotweed litter may have partially influenced the colonization of litter by aquatic fungi in a positive way.

Dry knotweed litter had the highest fungal biomass prior to placement in the streams (day 0 of the experiment), likely caused by colonization by phylloplane fungi prior to leaf abscission (Paul and Meyer 1996). Over time, though, nutrient-rich alder and FCL-poor cottonwood developed more fungal biomass while submerged than knotweed leaves. Our measure of fungal biomass, as estimated by ergosterol, did not differentiate between terrestrial and aquatic fungi species. Fungal biomass levels peaked after 31 days on alder and knotweed leaves, but levels on cottonwood peaked sometime after 56 days (at or after the end of the study). High concentrations of secondary compounds in the cottonwood leaves, such as high tannins which have been shown to have antimicrobial properties, could have led to the slow accumulation of fungal biomass during times when tannins were leaching from leaf tissues (LeRoy et al. 2007).

Macroinvertebrate abundance and diversity were not separately influenced by leaf species in this study, but overall community composition was influenced by both stream and leaf species. Shredders made up a smaller percentage of the invertebrate community on Bohemian knotweed leaves compared to native red alder leaves, but were similar to those on cottonwood leaves. Fewer shredders is consistent with reduced shredder species diversity found on Japanese knotweed leaves in France, which led to slower decomposition rates than native European alder (*Alnus glutinosa*) leaves (Dangles et al. 2002). Together, these results suggest that the influence of native species replacement by knotweed on stream ecosystem function may be exacerbated by the loss of benthic invertebrate shredders.

In the present study, differences in overall decay rates among species were very weak, even though there were strong species-level differences in leaf nutrient and structural properties. Decay rates were likely more affected by physical stream variables during the decomposition process than variables intrinsic to the leaf litter; however, differences in litter mass loss were observed at intermediate stages of decay. During the study, stream flows ranged from winter-time low flows to episodic bank-full flow events. Had flows been low for the entire study, which is unrealistic given the local climate, physical abrasion may have been minimized allowing litter quality to play a greater role in the decomposition process. Local climate (e.g., discharge regime) needs to be considered when predicting litter decomposition rates across large environmental gradients (Graça et al. 2010).

When comparing our rates of decay to other knotweed species (Table 4), we see that our rates are two- to four-fold higher than other studies, which was likely due to more physical abrasion during flood events (Bottollier-Curtet et al. 2011; Braatne et al. 2007; Chamberlain 2004; Dangles et al. 2002; Lecerf et al. 2007; Urgenson 2006; Urgenson et al. 2009). This study is the first to examine Bohemian knotweed, the genotypically diverse hybrid of Japanese and giant, and we intentionally collected knotweed leaves from five different sources distributed throughout southwest Washington to encompass relevant genetic variation. Bohemian knotweed has similar C levels compared to Japanese and giant, but generally lower N and P content and much higher lignin content. Litter decay rates are often reduced by high lignin concentrations (Hladyz et al. 2009; Schindler and Gessner 2009). In terms of biological decomposition, Bohemian knotweed leaves theoretically should decompose slower than Japanese knotweed leaves. However, in this study, physical factors were also important. Differences in leaf litter physio-chemical properties among the knotweed species could influence stream nutrient fluxes and ecosystem functions differently.

Table 4 Senesced knotweed leaf decay rates (*k*/day), nutrient, and lignin levels from published studies, including this study, among species and study locations

Location	Species	k/day	C %	N %	P %	C:N	C:P	Lignin %
France[a]	Japanese	0.0064	43.1	2.0	0.16	21.2	270.7	9.1
France[b]	Japanese	0.0092	47.6	0.99	0.044	48.1	1082	13.4
England[b]	Japanese	0.0135	47.4	1.82	0.119	26.0	398	13.7
France[c]	Japanese	0.0060						
Idaho[d]	Japanese[e]	0.0066		0.62	0.04			
Washington[f]	Giant		44.8	0.9		51.5		
Washington[g]	Bohemian	0.0269	44.4	0.86	0.05	63.2	893.3	30.8

[a] Bottollier-Curtet et al. et al. (2011)

[b] Lecerf et al. (2007)

[c] Dangles et al. (2003)

[d] Chamberlain (2004), Braatne et al. (2007)

[e] Species is reported to be Japanese, but it is most likely Bohemian (Gaskin et al. in review). At the time of the study, Bohemian was not well recognized

[f] Urgenson (2006), Urgenson et al. (2009)

[g] The present study

Changes in the quantities of litter inputs and the seasonal timing of inputs are other factors to be considered in order to better understand the impact of invasive knotweed on stream processes. This study measured litter quality, but did not address potentially significant issues of changes to litter quantity and timing as native riparian vegetation is replaced by knotweed. Bohemian knotweed drops all of its leaves in a 3–4 week period with the first hard frosts of late fall. In the Pacific Northwest, native deciduous shrubs and trees drop the majority of their leaves in the fall, over a 2–3 month period, and coniferous trees shed litter over even longer time periods. Other studies have found substantial changes in the quantity and timing of litter inputs to streams from the replacement of natural deciduous forests with exotic eucalyptus trees that resulted in reduced total organic matter inputs, but enhanced benthic storage of organic matter at eucalyptus invaded sites due to high inputs of twigs and bark during summer-time low discharge, as opposed to inputs of deciduous leaves during fall at higher discharges (Graça et al. 2002; Molinero and Pozo 2004).

Significant whole-stream responses to knotweed litter inputs may not be observed until a larger percentage of riparian areas are invaded by knotweed. In this study, stream sites were bordered by $\leq$50 % knotweed, the rest of the riparian vegetation being native plants. Our sites received a diverse input of litter types and qualities, as well as upstream nutrients and organic matter from relatively pristine headwaters. As long as there are sufficient nutrient and organic matter inputs to the stream, regardless of the sources, fungal and invertebrate communities may be able to effectively utilize a variety of organic matter types, including knotweed, as potential energy sources. As a consequence, ecosystem functions in streams may not be significantly affected until a certain threshold of knotweed invasion and subsequent litter input is reached. Indeed, the relatively early stage of knotweed invasion and hence its minor contribution to leaf litter standing crops may explain the absence of any stream functional responses between Japanese knotweed and native litter in a previous study (Braatne et al. 2007), whereas functional responses were observed in a more heavily invaded stream (Lecerf et al. 2007). These results emphasize the importance of upstream, headwater reaches in providing resources (organic matter, nutrients, and biota) to downstream reaches.

The influence of invasive species on litter decomposition appears to be independent of geographical origin (i.e., exotic or native) and more dependent on relative resource quality, as defined by chemical and structural traits of the leaf litter. Similar to this study, litter from exotic saltcedar (*Tamarix ramosissima*) in the southwestern U.S.A was of relatively poor quality and decomposed slower compared to native ash

(*Fraxinus velutina*), but was of higher quality and decomposed faster than native bulrush (*Scirpus americanus*) (Kennedy and Hobbie 2004). Other invasive exotics, such as *Rhododendron ponticum* in the British Isles and *Eucalyptus* species in Iberia, have poor quality leaf-litter and can influence litter decay rates and ecosystem functioning (Graça et al. 2002; Hladyz et al. 2011), whereas leaf-litter from the exotic, relatively high-quality, N-fixing albizia trees (*Falcataria moluccana*) in Hawaii enhanced decay rates, fungal biomass, and invertebrate abundances (MacKenzie et al. 2013). Native and exotic species with large stoichiometric imbalances and differences in litter quality are more likely to disrupt ecosystem functions.

The composition, productivity, nutrient uptake and decomposition of riparian plant communities affect nearly all aspects of stream ecosystem structure and function, from microbial biomass and activity to the flow of energy and nutrients to higher trophic levels. Because plant structural and functional traits control many of these fundamental processes (De Deyn et al. 2008), invasion-driven changes in plant community composition may be key factors influencing ecosystem traits, such as rates of material and nutrient fluxes. However, while it is likely that invasive plants may alter stream ecosystems, the direction and magnitude of these changes are not always predictable. Current management practices seek to control or eradicate non-native plant populations for the benefit of native fauna, since non-native plants are viewed as threats to wildlife habitat. Although restoration is becoming a widespread practice, the uncertainty in final results is rarely described prior to implementation. Very little is currently known about how knotweed invasions impact native fauna, and it remains unclear whether restoration practices targeting invasive plant removal actually improve habitat quality for resident animals (Cohen et al. 2012). Assessment of the ecosystem-level consequences of vegetation manipulation practices has been lacking and we do not have a clear understanding of what ecological responses govern the success of such restoration practices. We contend that establishing existing relationships between plants and less-obvious but important functions, such as nutrient immobilization, is an important prerequisite to evaluating the success of restoration efforts involving shifts in plant communities.

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