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Community and ecosystem consequences of giant knotweed (*Polygonum sachalinense*) invasion into riparian forests of western Washington, USA

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ABSTRACT

The invasive, non-native herb, giant knotweed (*Polygonum sachalinense*), is becoming increasingly common in riparian corridors throughout North America and Europe. Despite its prevalence, there has been limited study of its ecological impacts. We investigated the effects of knotweed invasion on the abundance and diversity of forest understory plants, and the quantity and nutrient quality of leaf-litter inputs, in riparian forests in western Washington, USA. Among 39 sampling locations, knotweed stem density ranged from 0 to 8.8 m^{-2}. Richness and abundance (cover or density) of native herbs, shrubs, and juvenile trees ($\leqslant$3 m tall) were negatively correlated with knotweed density. Where knotweed was present (>5.3 stems m^{-2}), litter mass of native species was reduced by 70%. Carbon:nitrogen ratio of knotweed litter was 52:1, a value 38–58% higher than that of native woody species (red alder [*Alnus rubra*] and willow [*Salix* spp.]). Resorption of foliar N prior to leaf drop was 76% in knotweed but only 5–33% among native woody species. By displacing native species and reducing nutrient quality of litter inputs, knotweed invasion has the potential to cause long-term changes in the structure and functioning of riparian forests and adjacent aquatic habitats.

1. Introduction

The spread of non-native plants into natural areas is receiving increasing attention from ecologists, conservationists, and land managers. Restoration initiatives that focus on reducing or eliminating invasive species can be time-consuming and expensive. Moreover, management is often undertaken without knowledge of the causes or ecological consequences of invasions (Byers et al., 2002). Management is often based on anecdotal evidence or subjective decisions that non-natives have adverse impacts (Blossey, 1999). Research on the ecological consequences of plant invasions is needed both to aid land managers in setting priorities for invasive species control and to enhance understanding of how species introductions and removals affect native communities and ecosystem processes.

The potential for individual species traits to structure community and ecosystem processes has been well documented (Lawton, 1994; Chapin et al., 1997). Most studies of non-native plant invasions focus on functional attributes of the invader as the primary determinant of ecosystem change (Levine et al., 2003). Chapin et al. (1996) suggest invaders which differ from resident species in a qualitatively novel trait (e.g., nitrogen fixation), are more likely to have significant effects on native systems. However, invaders can also have strong effects when they dominate ecosystem processes such as resource acquisition or litter production (Reinhart et al., 2006). These species have the potential to establish dense, monotypic stands that monopolize resources and displace native species (Mack et al., 2000; Dukes and Mooney, 2004) resulting in loss of critical structures and functions from these systems (Hooper and Vitousek, 1997; Chapin et al., 2000).

The ecological effects of invasion can be significant when non-natives displace foundation species—common or abundant species that dominate community structure and moderate or stabilize fundamental ecosystem processes (Ellison et al., 2005). Empirical evidence suggests that loss of foundation species can have cascading effects (Jenkins et al., 1999; Ellison et al., 2005). To fully understand these processes thus requires consideration not only of the traits of the invader, but also of the species that are displaced and their roles in ecosystem functioning. To our knowledge, few studies provide direct evidence of the ecological effects associated with displacement of foundation species by non-natives.

In this study we explore the community and ecosystem consequences of *Polygonum sachalinense* (giant knotweed) invasion into riparian forests of western Washington, USA. Knotweed has invaded low elevation floodplain corridors and tributary channels throughout North America and Europe, where it can form tall, dense stands that are difficult to eradicate. Concern over its invasion and

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the allocation of limited resources to its control are based largely on anecdotal evidence that knotweed is causing significant changes in the composition, structure, and function of riparian forests. Among these are displacement of native broadleaved (e.g., *Alnus rubra*) and coniferous species (e.g., *Tsuga heterophylla*) that regulate microclimate (Brosofske et al., 1997; Dong et al., 1998), stabilize stream banks and water flow (Bilby and Ward, 1991; Tabacchi et al., 1998), and provide energy and nutrients to aquatic macro-invertebrates (Cummins et al., 1973; Wallace et al., 1997; Naiman et al., 2005). However, there are few studies that quantify the ecological consequences of knotweed invasion in these riparian systems. We provide evidence for strong effects of invasion by quantifying relationships between knotweed density and various aspects of community structure and ecosystem functioning. We address two fundamental questions: (1) Does knotweed invasion alter the abundance and diversity of native understory species or reduce regeneration of dominant tree species? (2) What are the effects of invasion on quantity and nutrient quality of autumnal leaf-litter inputs into streams?

2. Methods

2.1. Study species

Giant knotweed (*P. sachalinense* F. Schmidt ex Maxim) is one of three closely related congeners that include Japanese knotweed (*Polygonum cuspidatum* Sieb. & Zucc.) and their hybrid, bohemian knotweed (*Polygonum* x *bohemicum* (Chrtek and Chrtková) (Zika and Jacobson, 2003). The three invade riparian areas, roadsides, and other disturbed habitats throughout North America and Europe (Beerling et al., 1994; Bailey, 2003; Barney, 2006). Giant and Japanese knotweed were first brought from Japan to Europe during the second half of the 19th century, and subsequently introduced to North America during the late 19th century as fodder and garden ornamental plants (Sukopp and Starfinger, 1995). According to floristic records, they are among the most rapidly spreading plant invaders in the northwest United States (Toney et al., 1998). Until recently, the three species were collectively referred to as Japanese knotweed throughout their introduced range (Bailey and Wisskirchen, 2006). The taxonomy of this group has been the subject of debate, and various authors place these species into the genera *Reynoutria*, *Polygonum*, or *Fallopia* (Child and Wade, 2000). We adhere to the *Polygonum* nomenclature because it is the most common usage in western North America (Zika and Jacobson, 2003).

Phenological, morphological, and chemical properties of knotweed appear to facilitate its invasion success. It is a rhizomatous perennial often reaching 5 m in height, with long (30–50 cm) cordate leaves and hollow ligneous stems (Sukopp and Starfinger, 1995). Its biomass can exceed 200 tons/ha, with a leaf area index of 21 and energy content of 12,000 MJ/ha, values exceeding any other herbaceous vegetation in the world (Sukopp and Starfinger, 1995). Knotweed emerges early in the growing season, when growth increments can reach 15 cm/day (Sukopp and Starfinger, 1995). Additionally, it produces novel secondary compounds which may contribute to allelopathic or antimicrobial effects (Inoue et al., 1992; Weston et al., 2005). Throughout its introduced range, knotweed's primary mode of reproduction is through prolific vegetative spread from rhizome or stem fragments (Pyšek et al., 2003). However, recent evidence suggests reproduction from seed may play are larger role in dispersal than previously assumed (Forman and Kesseli, 2003; Bailey et al., 2007; Gammon et al., 2007; Grimsby et al., 2007; Tiebre et al., 2007). Once introduced, it can spread rapidly through the riparian zone as flood waters transport rhizome fragments downstream (Bímová et al., 2003).

2.2. Study area

This study was conducted along Grandy Creek (48°33′N, 121°49′W), a tributary of the mid- to lower Skagit River in the Puget Sound lowlands of Washington State, USA. Grandy Creek is 3–10 m wide and flows as a meandering, braided channel for ~12 km before reaching the Skagit. The Skagit basin is characterized by a temperate, maritime climate. Average monthly maximum and minimum temperatures are 15 °C (August), and 5 °C (January). Annual precipitation averages 182 cm of which 68 cm falls as snow (climate-station data from nearby Concrete, WA; 59 m elevation; 1931–2005, Western Regional Climate Center http://www.wrcc.dri.edu/summary/climsmwa.html).

The study reach spanned ~1 km in length. Sampling was limited to low terrace and floodplain forests adjacent to the active channel—habitats most commonly invaded by knotweed (Dawson and Holland, 1999; Collingham et al., 2000; Bímová et al., 2004). Pioneer broadleaved trees, primarily red alder (*A. rubra*), but also willow (*Salix* spp.) and some black poplar (*Populus trichocarpa*) dominated the overstory. Overstory conifers were less common and included western red cedar (*Thuja plicata*), Douglas-fir (*Pseudotsuga menziesii*), and western hemlock (*T. heterophylla*). Salmonberry (*Rubus spectabilis*), thimbleberry (*Rubus parviflorus*), vine maple (*Acer circinatum*) and sword fern (*Polystichum munitum*) were common understory species. Knotweed was the dominant non-native species. Species-level identification of willow could not be made consistently in the absence reproductive structures and may have included several taxa (*Salix lucida, S. sitchensis,* and *S. scouleriana*). Nomenclature follows Hitchcock and Cronquist (1973).

2.3. Composition and abundance of riparian understory vegetation

In July and August 2004, we sampled understory vegetation in forest patches characterized by varying levels of knotweed invasion. Thirty-nine, 2 × 10 m belt transects were placed perpendicular to the stream channel at random locations at least 10 m apart. Within each transect, densities of knotweed stems, shrubs, and juvenile trees (⩽3.0 m tall) were tallied by species. In addition, we randomly placed two 1-m^2 quadrates within which we estimated cover of each herbaceous species by cover class: 1–4, 5–25, 26–50, 51–75, 76–95, and >95% (Mueller Dombois and Ellenberg, 1974).

Overstory attributes and environmental factors known to influence understory vegetation were also measured within each transect to test whether these might explain, or contribute to, observed relationships between knotweed density and resident species. Overstory attributes included canopy cover (%) and basal area (m^2/ha) of trees >5 cm dbh (diameter at breast height). Canopy cover was estimated by cover class (as above) at two random locations using a densiometer; estimates were then averaged for each transect. Basal area was calculated using the point-quarter-method (Mueller Dombois and Ellenberg, 1974); sample points were centered at 2.5 m from the ends of each transect. Environmental factors included height (m) above the wetted channel and slope (%).

2.4. Quantity and nutrient quality of litterfall

Quantity of autumn litterfall was measured adjacent to a subset of transects that represented strongly contrasting levels of invasion: seven "invaded" sites with a relatively high density of knotweed (>5.3 stems m^{-2}; mean of 7.3 stems m^{-2}) and seven "non-invaded" sites with little or no knotweed (⩽0.75 stems m^{-2}; mean of 0.17 stems m^{-2}). Transects were selected to encompass a range of overstory and environmental conditions. At each location, three 38 × 60 cm traps were placed on the ground, ⩽2 m from the