



Differential allelopathic effects of Japanese knotweed on willow and cottonwood cuttings used in riverbank restoration techniques



Fanny Dommanget^{a,b,*}, André Evette^a, Thomas Spiegelberger^a, Christiane Gallet^c, Marine Pacé^a, Marika Imbert^a, Marie-Laure Navas^d

^a Irstea, EMGR, Research Unit Mountain Ecosystems, 2 rue de la Papeterie, BP 76, F-38402 Saint-Martin-d'Hères, France

^b AgroParisTech, ENGREF, Research Unit Mountain Ecosystems, 2 rue de la Papeterie, BP 76, F-38402 Saint-Martin-d'Hères, France

^c Laboratoire d'Ecologie Alpine, CNRS UMR 5553, Université de Savoie, 73376 Le Bourget du Lac, France

^d Montpellier SupAgro, Centre d'Ecologie Fonctionnelle et Evolutive (UMR 5175), 1919 Route de Mende, 34293 Montpellier Cedex 5, France

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ABSTRACT

Using bioengineering techniques to restore areas invaded by *Fallopia japonica* shows promising results. Planting tree cuttings could allow both rapidly re-establishing a competitive native plant community and reducing *F. japonica* performance. However, *F. japonica* has been shown to affect native plant species through different mechanisms such as allelopathy. This article investigates the phytotoxic effect of *F. japonica* on the resprouting capacity and the growth of three *Salicaceae* species with potential value for restoration. An experimental design which physically separates donor pots containing either an individual from *F. japonica* or bare soil from target pots containing cuttings of *Populus nigra*, *Salix atrocinerea* or *Salix viminalis* was used. Leachates from donor pots were used to water target pots. The effects of leachates were evaluated by measuring the final biomass of the cuttings. *F. japonica* leachates inhibited the growth of cuttings, and this effect is linked to the emission of polyphenol compounds by *F. japonica*. Leachates also induced changes in soil nitrogen composition. These results suggest the existence of allelopathic effects, direct and/or indirect, of *F. japonica* on the growth of *Salicaceae* species cuttings. However, the three species were not equally affected, suggesting that the choice of resistant species could be crucial for restoration success.

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1. Introduction

Biological invasions are considered as one of the global changes threatening biodiversity worldwide (Thuiller, 2007). Nevertheless, only a small portion of introduced plants spread extensively and become invasive in their new range (Hayes and Barry, 2008; Williamson, 1993). The search for the mechanisms explaining the success of invasive species raises a great deal of interest among the scientific and management communities as better identification of these processes is crucially needed to design appropriate management actions to limit their impacts and their spread.

Several hypotheses have been proposed to explain the success of invasive plants. Some successful exotic plants have intrinsic characteristics such as a high resource uptake and use efficiency associated with a high growth rate, allowing them to take advantage in

resource-rich environments (Blossey and Notzold, 1995; Davis et al., 2000; Elton, 1958). Moreover, in the invaded environment competition for resources could be influenced by additive mechanisms favouring the introduced species. For example, the absence of their natural enemies releases alien plants from trophic pressure and gives them the opportunity to express their full competitive potential (Elton, 1958; Keane and Crawley, 2002). Evidence is also growing supporting the novel weapon hypothesis, which assumes that some invasive plants produce allelochemicals to which native species are naïve and therefore particularly sensitive (Callaway and Aschehoug, 2000; Hierro and Callaway, 2003). Allelopathy is the mechanism of the novel weapon hypothesis which has also been designated as the allelopathic advantage against resident species (Callaway and Ridenour, 2004). Allelopathy is here considered as only the negative effects, either direct or indirect, of one plant on another through production of a compound or a group of compounds, as Inderjit and Duke (2003) suggested and because it is a commonly accepted definition in plant ecology (Abhilasha et al., 2008; Callaway et al., 2008; Hierro and Callaway, 2003; Murrell et al., 2011; Viard-Crétat et al., 2009).

* Corresponding author. Irstea, Research Unit Mountain Ecosystems, 2 rue de la Papeterie, BP 76, F-38402 Saint-Martin-d'Hères, France. Tel.: +33 476 76 28 65.

E-mail address: fanny.dommanget@irstea.fr (F. Dommanget).

The role of allelopathy in invader superiority has been tested successfully on different plant genera (Grove et al., 2013; Jarchow and Cook, 2009; Sharma et al., 2005; Thorpe et al., 2009). Some exotic species can affect the recruitment of native species through the reduction of seed germination (Sharma et al., 2005) or affect adult performance by reducing plant growth. For example, Thorpe et al. (2009) showed that adding (\pm)-catechins, which are produced by the invasive *Centaurea maculosa* in the rhizosphere of target plants, reduces the growth of species from the invaded range (USA) but not of species from the native range (Romania). Interestingly, reducing the allelopathic effect of the invasive *Typha angustifolia* in the soil reverses the competitive outcome between *T. angustifolia* and the native *Bolboschoenus fluviatilis*, demonstrating the importance of allelopathy in the success of this exotic species (Jarchow and Cook, 2009). *Fallopia japonica* [Houtt.] Ronse Decraene, or Japanese knotweed, is considered as one of the worst invasive plants in the world (Lowe et al., 2000). *F. japonica* has often been observed to form dense and almost mono-specific stands (Aguilera et al., 2010), leading to the conclusion that allelopathy may be an explanation for its remarkable success. Some studies already suggest a phytotoxic effect of *F. japonica* and its congeners (*Fallopia sachalinensis* and *Fallopia X bohemica*) on native plants (Murrell et al., 2011; Siemens and Blossey, 2007; Vrchatová and Šerá, 2008) because of phytotoxic compounds (including anthraquinones and other polyphenols) in their root leachates (Fan et al., 2010; Meiffren et al., 2010; Vastano et al., 2000). This process could play a major role in the invasion of *Fallopia* ssp. combined with other factors such as resource pre-emption (Siemens and Blossey, 2007) and modification of nutrient cycles (Dassonville et al., 2011). This paper aims to investigate the allelopathic properties of *F. japonica* and its effects on tree cuttings used in restoration.

Initially imported from Asia during the 19th century for ornamentation, *F. japonica* is now invasive in many ecosystems in Europe and North America (Bailey, 2005). It affects ecosystems by forming a dense canopy, reduces the floral (Bímová et al., 2004; Maurel et al., 2010) and faunal (Gerber et al., 2008; Maerz et al., 2005) biodiversity and modifies nutrient cycles (Dassonville et al., 2011). This species is mostly found along riparian habitats, which assume important ecological functions (Naiman et al., 1993), and spreads mainly by a rapid clonal growth (Bímová et al., 2003; Pyšek et al., 2003; Tiébré et al., 2007). Regeneration from rhizome fragments is very efficient as a few grams of rhizome are sufficient for rapid production of a new stand (Brock and Wade, 1992; Sásik and Eliáš, 2006). The high cost of eradicating *F. japonica* (e.g. estimated costs linked with Asian knotweed management and impacts exceed 260 Million \$US/year in the UK, Williams et al., 2010) compels practitioners to find economical and efficient ways to restore ecosystems (Crowhurst, 2006).

Various methods have been tested to control *F. japonica*. Herbicides have shown their limitation (Bashtanova et al., 2009) and are forbidden or not recommended along rivers where the herbicide could leach into the water. Cutting and mowing are solutions commonly used to eradicate or at least to reduce *F. japonica* vigour in conservation areas, but they are labour-intensive and therefore expensive (Delbart et al., 2012; Gerber et al., 2010; Seiger and Merchant, 1997). Restoring invaded habitats by stimulating successional processes through seeding and/or transplanting native species can be a solution for both the conservation of native communities and the control of invasive species (Sheley and Smith, 2012). Such alternative strategies have already been successfully tested against various herbaceous invasive plants (Ammond et al., 2013; Cutting and Hough-Goldstein, 2012; Larson et al., 2013). For *F. japonica*, planting *Salicaceae* cuttings is a promising solution. Already tested sporadically by managers, restoration projects of

F. japonica invaded habitat using tree cuttings have had variable success (Barták et al., 2010; Delbart et al., 2012; Deschamps, 2010; Masson, 2002; Toews, 2012). Despite the promising outcomes of such techniques (restoration associated with resistance to invasion), no underlying mechanisms have been tested that could explain the fluctuating outcome.

Allelopathy could be one mechanism involved in failures of restoration experiments, by limiting growth of competing species. Previous studies of allelopathy by the *Fallopia* complex have all used controversial designs (Inderjit and Callaway, 2003). Laboratory studies on seed germination with identified allelochemicals extracted from the rhizome or the stem of *F. japonica* (Fan et al., 2010; Vrchatová and Šerá, 2008) do not replicate the natural concentration of these molecules, whereas other studies which apply activated charcoal (Murrell et al., 2011; Siemens and Blossey, 2007) are controversial because this substance can also alter soil pH and nutrient availability (Lau et al., 2008). In this study, we chose to test the allelopathic potential of *F. japonica* on *Salicaceae* species in greenhouse conditions by means of an original semi-controlled experiment where donor and target pots are separated physically to discriminate resource competition from allelopathy. This design is built on previously cited studies in an effort to simulate conditions closer to the natural situation and to explicitly address chemically mediated interactions (Viard-Crétat et al., 2009). In addition, to our knowledge, no experiment directly addresses the role of allelopathy in cutting – development success.

We chose to assess the impact of *F. japonica* leachate on the resprouting capacity and growth of three species from the two genera represented in the *Salicaceae* family: *Salix viminalis* L., *Salix atrocinerea* Brot. and *Populus nigra* L. We address the following questions: (1) does *F. japonica* leachate limit the growth of *Salicaceae* cuttings? (2) are target species equally affected? and (3) can these effects be directly linked to polyphenol emission or are they mediated by changes in soil properties?

2. Material and method

2.1. Experimental design

The experimental design adapted from Newman and Rovira (1975) and Viard-Crétat (2009) involved “donor pots” and “target pots” to discriminate resource competition effects from allelochemical effects (Fig. 1) in a factorial balanced design. In donor pots, either a *F. japonica* individual was planted or bare ground was left; in the target pots, one cutting of the three different target species was planted. Pots were organised so that target pots were irrigated with donor pot leachate by gravity.

The experiment included 58 pairs of one donor pot connected to one target pot, i.e. 116 pots, and was conducted in greenhouse conditions near Grenoble (France). Mean daily temperatures recorded during the experiment ranged from 8 to 31 °C. Donor pots and target pots (volume 6 L) were filled with a soil mixture (4/6 of sand, 1/6 of vermiculite-perlite and 1/6 of potting soil) to guarantee homogeneity between pots and to combine a high ability to drain and evacuate the leachate (sand properties) and a water and nutrient (vermiculite, perlite and potting soil properties) retention potential. All pots were watered several times before the experiment started in order to wash out polyphenols contained naturally in initial potting soil.

Donor pots had a 14-cm-wide opening on the bottom in which a plastic funnel (\varnothing 15 cm) was put. On the top of the funnel, two meshes with different sizes (5 mm and 2 mm) were superposed to retain the soil. The funnel was connected to a polyethylene (PE) tube through which the leachate flowed to the target pot. Each donor pot was linked to a single fixed target pot. The place of each

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