



Original article

Effects of seed traits variation on seedling performance of the invasive weed, *Ambrosia artemisiifolia* L.

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ARTICLE INFO

Article history:

Received 19 November 2015
 Received in revised form
 14 January 2016
 Accepted 15 January 2016
 Available online 24 January 2016

Keywords:

Achene variability
 Competitive ability
 Cotyledon area
 Phenotypic plasticity
 Seed colour
 Seed mass

ABSTRACT

Seedling performance can determine the survival of a juvenile plant and impact adult plant performance. Understanding the factors that may impact seedling performance is thus critical, especially for annuals, opportunists or invasive plant species. Seedling performance can vary among mothers or populations in response to environmental conditions or under the influence of seed traits. However, very few studies have investigated seed traits variations and their consequences on seedling performance. Specifically, the following questions have been addressed by this work: 1) How the seed traits of the invasive *Ambrosia artemisiifolia* L. vary among mothers and populations, as well as along the latitude; 2) How do seed traits influence seedling performance; 3) Is the influence on seedlings temperature dependent. With seeds from nine Western Europe ruderal populations, seed traits that can influence seedling development were measured. The seeds were sown into growth chambers with warmer or colder temperature treatments. During seedling growth, performance-related traits were measured. A high variability in seed traits was highlighted. Variation was determined by the mother identity and population, but not latitude. Together, the temperature, population and the identity of the mother had an effect on seedling performance. Seed traits had a relative impact on seedling performance, but this did not appear to be temperature dependent. Seedling performance exhibited a strong plastic response to the temperature, was shaped by the identity of the mother and the population, and was influenced by a number of seed traits.

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1. Introduction

The juvenile stage represents the most vulnerable period in a plant's life cycle (Simons and Johnston, 2000; Vange et al., 2004). During this time, seedling performance is crucial and can have an impact on later life stages, and therefore affect the overall fitness of the parents (Gross, 1984; Renata D Wulff, 1986). The successful establishment of a seedling increases the chances for effective establishment of opportunist species or plant invaders in new areas (Fenesi et al., 2014; Skálová et al., 2012). It is therefore very important to understand what the factors are that can influence seedling performance. Variation in such performance may result from genetic variation (Biere, 1991), have a plastic origin in response to environmental conditions (Hotchkiss et al., 2008), or be caused by seed trait variation (Dolan, 1984; Harper et al., 1970; Monty et al., 2013; Roach and Wulff, 1987; Stanton, 1984).

Seed traits, e.g., seed mass, seed size, seed colour, are known to vary considerably within various species, even among populations or individuals (Harper et al., 1970; López et al., 2008; Roach and Wulff, 1987; Simons and Johnston, 2000; Stanton, 1984; Susko and Lovett-Doust, 2000). This phenotypic variation often comes about from environmental constraints. For example, evidence has been found of clinal variations in seed traits as a consequence of local climatic conditions (Moles et al., 2007; Monty and Mahy, 2009). When the resources become limiting, a variation may appear because of trade-offs in resource allocation between seed size and seed number (Smith and Fretwell, 1974; Venable, 1992). This differential resource allocation is known as the "bet-hedging" strategy.

A large intraspecific variation in seed traits can also be an adaptive response of the plant to environmental conditions, e.g. to habitat characteristics (Tautenhahn et al., 2008), to the competition intensity (Kleunen et al., 2001), or to predation (Moegenburg, 1996). Selection can also directly promote seed variation in order to enhance the ability of a plant to survive in a wider range of environmental conditions (Fenner and Thompson, 2005). The

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production of a 'range' of seed traits is an effective evolutionary strategy that can minimize risk and increase the probabilities of reproducing in an unpredictable environment (Venable and Brown, 1988). This is particularly true for annual ruderal plant species that colonize disturbed habitats (Harper, 1977).

The consequences of seed trait variation on seedling performance may depend on environmental conditions experienced by the progeny, with performance differences between large and small seeds being greatest under adverse conditions and lower in more favourable environments (Dolan, 1984; Gross and Smith, 1991; Gross, 1984; Monty et al., 2013; R D Wulff, 1986a, 1986b). These differences would be explained by a stronger advantage of seed resources in aiding seedling development in adverse conditions versus favourable conditions where the seedlings are less stressed.

Seed traits may have different influence on seedling development. For example, seed mass may be considered a proxy of the reserves that the mother had provided to the embryo, and it is often used to account for seed variation (Simons and Johnston, 2000; Vange et al., 2004). Seed mass variation can be directly connected to germination kinetics (Harper et al., 1970; Schutte et al., 2008), but may also have an impact on seedling performance (Baskin and Baskin, 2001; Dolan, 1984; Harper et al., 1970; Monty et al., 2013; Roach and Wulff, 1987; Stanton, 1984). Another example is seed colour that has been documented to be linked to seed dormancy, with darker or more coloured seeds having a thicker seed coat and a greater dormancy than lighter seeds (Durán and Retamal, 1989; Khan et al., 1997; Powell, 1989; Wyatt, 1977). The seed coat exerts its germination-restrictive action most of the time by being impermeable to water and/or oxygen, by its mechanical resistance to radicle protrusion, or by the presence of phenolic compounds with antioxidant properties that play a protective role against degradation processes (Debeaujon et al., 2000).

The study of seed traits variation is especially important in the case of plant invasion. The seed is often the dispersal vector of invasive plant (Cain et al., 2000), and is then to the invasion process. Seed trait variation could be a major feature explaining invasive plant success, as it not only can enhance colonization at both local and regional scales, but also facilitate the exploitation of spatial and temporal heterogeneous environments (Mandák and Pyšek, 2001; Monty et al., 2013; Willis and Hulme, 2004). A better understanding of how plant invaders colonize and establish in new areas is therefore critical to prevent further invasion. However, to date, just a few studies have examined the influence of seed variation and its consequences for plant invaders (Söber and Ramula, 2013; Susko and Lovett-Doust, 2000).

Ambrosia artemisiifolia L. (common ragweed, Asteraceae) is an annual plant that was introduced from North America to Europe more than a century ago (Heckel, 1906). The achenes of *A. artemisiifolia* have a central terminal beak surrounded by a ring of tiny spines (Fig. 1), probably having a dispersal role through soils and human transport (Bassett and Crompton, 1975). The species substantially spread in numerous European countries (Chauvel et al., 2006; Kazinczi et al., 2008; Smith et al., 2013; Solomon et al., 2007). It is both a weed colonizing spring crops and a ruderal plant invading open disturbed habitats, such as wastelands, roadsides or riverbanks (Bassett and Crompton, 1975). For convenience, the entire dispersal unit of *A. artemisiifolia* will be referred to as a seed.

A. artemisiifolia invasion in Europe is an especially interesting case study, as invasion success is known to be linked to seed characteristics (Fenesi et al., 2014; Fumanal et al., 2008; Guillemin and Chauvel, 2011). On top of being highly variable (Fumanal et al., 2007a; Gebben, 1965), the seeds are able to survive for many years in the soil (Bassett and Crompton, 1975), allowing the creation of a long-lasting soil seed bank. This soil seed bank ensures the



Fig. 1. Standard image of a seed of *Ambrosia artemisiifolia* taken to measure seed functional area and seed coat lightness. The red-dashed ellipse represents an example of the largest ellipse that could be drawn inside the seed for functional area measurement. Scale bar = 1 mm. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

establishment of the species for years beyond once a single successful seed production has occurred in the area (Fumanal et al., 2008). Furthermore, the species produces allergenic pollen known to be causing a health crisis in Europe, making the understanding of the mechanisms involved in invasion success highly valuable for management (Kazinczi et al., 2008; Laaidi et al., 2003; Smith et al., 2013).

Both studying how seed variation is structured as well as gaining insight into its consequences on seedling performance are essential to better comprehend the critical factors influencing seedling development in the early stage of its life, and the subsequent successful establishment of the species. Specifically, the work presented here addressed the following questions: 1) How is the seed variation structured among mothers and populations and are there geographic patterns? 2) How do seed traits influence seedling performance? 3) Is the influence of seed traits on seedling performance dependent on environmental conditions (i.e. the temperature)?

2. Materials and methods

2.1. Seed collection

Seeds of *A. artemisiifolia* were collected from nine populations in the Netherlands, Belgium and France (Table 1). Populations were sampled in ruderal habitats (along roadsides, riverbanks or wastelands) during the autumn of 2013. In each population, all seeds of ten randomly chosen mature individuals (i.e. mother plant) having at least 30 seeds were collected and stored in separate paper bags. Pending the start of the experiment, the seeds were stored for 6 months at 4 °C.

Table 1
Provenances of the sampled populations of *Ambrosia artemisiifolia*.

Latitude (°N)	Longitude (°E)	City	Country	Code
51.23493	4.43645	Merksem	Belgium	A
51.12004	5.84034	Echt	Netherlands	B
50.92290	3.21370	Izegem	Belgium	C
47.00574	4.84703	Beaune	France	D
46.29726	4.83344	Mâcon	France	E
45.96413	5.25703	Châtillon-la-Palud	France	F
44.74784	4.91819	Ramière	France	G
44.43927	4.67990	Donzère	France	H
44.09044	4.73589	Montfaucon	France	I

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