# Effects of the seed weight and burial depth on the seed behavior of common ragweed (Ambrosia artemisiifolia)

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RESEARCH PAPER

# Effects of the seed weight and burial depth on the seed behavior of common ragweed (*Ambrosia artemisiifolia*)

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Common ragweed (*Ambrosia artemisiifolia* L.) is one of the annual plants that were described recently as invasive weeds in Europe. This species is described as an invasive plant that produces seeds that are highly variable. Its production of variably sized seeds is regarded as promoting its spread in different environments. Experiments were carried out to determine the influence of the seed weight and temperature on germination and the influence of the seed weight and burial depth on seedling emergence. The seeds were divided into a number of classes of weight and the seed weight effect on germination was evaluated by Petri dish assays. In another experiment, the seeds were buried at different depths in a clay soil/sand mix to estimate the burial effect on germination and seedling emergence. The germination level of *A. artemisiifolia* was high overall, between 76.8% and 94.2%. The seed germination was modified by temperature but it was not influenced by the seed weight. The amounts of germination and seedling emergence were greater for the seeds on the soil surface and decreased with an increasing burial depth, from 2 to 8 cm. No germination or emergence was observed for the seeds that were buried at 10 and 12 cm. The lightest seeds were more sensitive to burial. A greater level of seedling emergence for those seeds that were placed near the soil surface could explain the success of this species in open habitats, where the probability of deeper burial is low. After high seed production, the management of *A. artemisiifolia* in fields could be partly achieved through soil tillage, burying seeds below 10 cm, and not carrying out deep soil tillage the following year.

**Keywords:** burial depth, common ragweed, germination, seed weight, seedling emergence, temperature.

Common ragweed (*Ambrosia artemisiifolia* L.) is an abundant weed that is native to North America (Basset & Crompton 1975). This species was introduced into Europe, including France, at the end of the 1900s (Chauvel *et al.* 2006) and is now present in several European countries, including Ukraine (Song & Prots 1998), Hungary (Török *et al.* 2003), and Switzerland (Bohren *et al.* 2006). In France, common ragweed now is considered as an invasive species that occurs widely in disturbed habitats (Basset & Crompton 1975) and fields (Chollet *et al.* 1998). Its large ecological breadth enables it to be a successful pioneer in early successional ecosystems and in several types of environment (Fumanal *et al.* 2008). As its pollen is highly allergenic, the fast spread of *A. artemisiifolia* now causes an important public health problem (Touraine *et al.* 1965). Besides, this weed can be strongly competitive in summer annual crops (Chollet *et al.* 1998), in which it can be observed at high densities. This plant is now considered by French farmers to be one of the most problematic invasive weeds in spring crops.

In order to improve its control and to contain the spread of *A. artemisiifolia*, it is essential to have a wider

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biological knowledge of the plant. Seed germination and seedling emergence are crucial phases in its life history. Its germination strategy is partly known (Bazzaz 1979): the seeds of this annual species are dormant at maturity and require stratification in order to germinate. However, *A. artemisiifolia* seeds can enter complete secondary dormancy after exposure to the sequence of natural temperature regimes in spring (Baskin & Baskin 1980). Bazzaz (1979) considered that this induction of secondary dormancy in *A. artemisiifolia* is a strategy to protect the seeds in the seed bank until the conditions are again favorable for germination.

The seed weight is widely recognized as a key plant trait in plant population dynamics and community structure (Turnbull *et al.* 2004) and this biological characteristic is highly variable for *A. artemisiifolia* (Washitani & Nishiyama 1992; Fumanal *et al.* 2007). The seed production of *A. artemisiifolia* also varies considerably. It was observed that the weight of its seeds was negatively correlated with the seed number per plant (McKone & Tonkyn 1986). The variability of the seed weight often is cited as a favorable trait for invasive species that have to be able to cope with a range of different environmental conditions (Banovetz & Scheiner 1994). While lighter seeds often are associated with a greater dispersal and higher persistence in the seed bank (Harper *et al.* 1970), heavier seeds are considered to be better adapted for competitive conditions (Fenner & Thompson 2005). Daws *et al.* (2007) also found that an increasing seed weight could confer a higher level of competitiveness for invasive species in California, USA. Thus, variability in the seed weight could be important in the spread and competitive success of an invasive plant. Forcella (1985) also suggested that those species with a higher spread rate often have relatively rapid seed germination.

In order to better understand the present success of this annual species in disturbed habitats with high selective pressure (e.g. tillage and herbicide use), the aim of this study was to assess the impact of the seed weight and burial depth on the establishment of *A. artemisiifolia* populations.

## MATERIALS AND METHODS

### Plant material

One population of *A. artemisiifolia* that had been harvested in a field crop in Pluvet, eastern France, in 2005 was used to describe the seed behavior. The seeds were harvested from at least 50 plants at maturity. After harvest, all the seeds were stored in dry conditions at 4°C. Prior to the experiment, the seeds were placed on blotter paper (160 g $m^{-2}$; Germaflor, Aalsmeer, the Netherlands) that was moistened with deionized water in Petri dishes and received a cold treatment for 3 weeks in darkness at 4°C (±0.5°C) in order to remove the primary dormancy.

### Effects of the seed weight on seed germination

Three-hundred seeds were weighed individually. The seed weight ranged from 1.2 to 7.7 mg and the values of the median (3.98 mg) and mean (4.08 mg) weight of the seed were similar. The 300 seeds were divided into five classes of identical numbers: light (LL): ≤3.1 mg; medium light (ML): >3.1 mg to ≤3.7 mg; medium (MM): >3.7 mg to ≤4.3 mg; medium heavy (MH): >4.3 mg to ≤5 mg; and heavy (HH): >5 mg.

These experiments were carried out through the months of March, April, and May 2006. Fifty seeds were arranged in each 90 mm-diameter glass Petri dish. Five replicate Petri dishes were used per treatment and all the Petri dishes were placed in a randomized complete-block design. The germination paper (3645; Whatman International, Maidstone, UK) was moistened initially with 4 mL of 0.2% $KNO_3$ solution to remove the primary dormancy of the seeds. The Petri dishes were placed in a growth chamber (KBW 240 and KBW 400; Binder, Tuttlingen, Germany) at fluctuating day/night temperatures of 15/10°C and 25/15°C with a 16 h day/8 h night photoperiod. The seeds were checked for germination every day for 21 days. The seeds were considered to have germinated when the radicle exceeded 1 mm. The germinated seeds were removed from the Petri dishes. At the end of the experiment, the ungerminated seeds were crushed individually so as to check whether or not they were empty. The crush test shows if the seeds are intact (Sawma & Mohler 2002). The empty seeds were eliminated in order to calculate the germination percentage of the seeds. All the empty seeds were present in the LL weight class (data not shown). The cumulative germination was modeled by using the logistic function, $Y = a/(1 + b \times \exp[-cX])$, with $X$ referring to the time (number of days) and $Y$ referring to the germination percentage. The germination rate (per day) was calculated as the reciprocal time ($1/t_{50}$) that was required to achieve 50% of total germination of the seeds.

### Effects of the seed burial depth on germination and seedling emergence

The number of weight classes was reduced to three, taking into account the results of the germination experiment: light (L): ≤3.1 mg; medium (M): >3.1 mg to ≤5 mg; and heavy (H): >5 mg. The seeds were placed in containers (42 cm × 28 cm × 16 cm). Three weight classes and six depths were tested. For each treatment, four replicates were set up. One depth was tested in a container. Each container was a replicate, containing 22 seeds of the same weight class, and was filled with 18 L of clay soil/sand mix (1:1 v/v). After stratification, the seeds were placed on the surface (0 cm) or planted 2, 4, 8, 10, and 12 cm deep. The containers were irrigated initially to field capacity and then were irrigated during the experiment to maintain field capacity. The seeds were sown on 18 April 2006 in a greenhouse at a fluctuating day/night temperature of 25/17°C.

The number of seedlings that emerged was recorded daily for 25 days. The seedlings were considered to have emerged when the cotyledons were visible. At the end of the experiment, the unemerged seeds were dug out to determine the number of germinated (unemerged), dormant, and empty seeds. It was considered that the experiment's duration did not allow for the disintegration of embryo germinated seeds (unemerged). The germination percentage of the seeds was calculated after the empty seeds were eliminated.

### Statistical analysis

The data on germination (% and rate) and seedling emergence (%) were analyzed by a *t*-test and an ANOVA. The SAS software (SAS Institute, Cary, NC, USA) was used for the statistical analysis. All the data on germination and seedling emergence were arcsine square root-transformed before the analysis. If the ANOVA showed significant differences, Tukey's Honestly Significant Difference test was used to identify the homogeneous groups. Significant differences among the treatments were considered to be at $P < 0.05$. The untransformed data are indicated in the figures.

## RESULTS

### Effects of the temperature and seed weight on germination

The stratification treatment and $KNO_3$ solution application were applied to break the primary dormancy of the seeds. The level of seed germination was high, with at least 76.8% for the ML seeds at the fluctuating day/night temperature of 15/10°C (Fig. 1a). The mean germination was assessed for both temperature conditions (fluctuating 15/10°C and 25/15°C) and it was found that the germination level was significantly different for both temperature conditions (80.3% ± 4.04 for 15/10°C and 90.6% ± 4.8 for 25/15°C) (Table 1 & Fig. 1a). However, the germination rate was not significantly modified by temperature (0.147 ± 0.019 for 15/10°C and 0.139 ± 0.014 for 25/15°C) (Table 1 & Fig. 1b). The seed weight had no influence on the germination of the seeds under

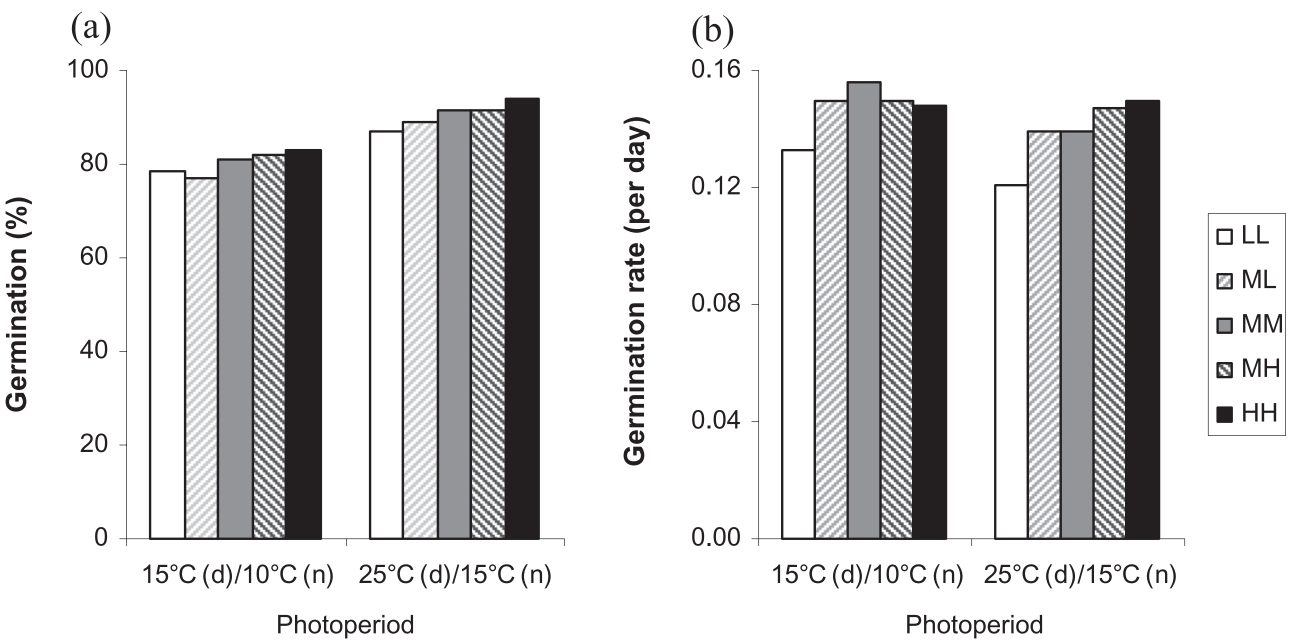


**Fig. 1.** (a) Germination percentage and (b) germination rate of *Ambrosia artemisiifolia* seeds of the Pluvet (2005) population for five weight classes (light [LL], medium light [ML], medium [MM], medium heavy [MH], and heavy [HH]) at fluctuating day (d)/night (n) temperatures.

**Table 1.** Two-factor ANOVA for the effects of the temperature and seed weight on the germination percentage and germination rate of *Ambrosia artemisiifolia* from the Pluvet (2005) population

| Variable | Sum of squares | d.f. | *F*-value | *P*-value |
|---|---|---|---|---|
| Germination | | | | |
| Temperature | 0.2340 | 1 | 56.00 | <0.001 |
| Seed weight | 0.0290 | 4 | 1.73 | 0.162 |
| Temperature × seed weight | 0.0200 | 4 | 1.20 | 0.326 |
| Residual | 0.1670 | 40 | | |
| Germination rate | | | | |
| Temperature | 0.0008 | 1 | 2.64 | 0.111 |
| Seed weight | 0.0032 | 4 | 2.57 | 0.052 |
| Temperature × seed weight | 0.0005 | 4 | 0.41 | 0.801 |
| Residual | 0.0120 | 40 | | |

**Table 2.** Two-factor ANOVA for the effects of the burial depth and seed weight on the germination and seedling emergence of *Ambrosia artemisiifolia* from the Pluvet (2005) population

| Variable | Sum of squares | d.f. | *F*-value | *P*-value |
|---|---|---|---|---|
| Germination | | | | |
| Burial depth | 21.46 | 5 | 119.95 | <0.001 |
| Seed weight | 0.85 | 2 | 11.86 | <0.001 |
| Burial depth × seed weight | 1.41 | 10 | 3.95 | <0.001 |
| Residual | 1.93 | 54 | | |
| Seedling emergence | | | | |
| Burial depth | 24.52 | 5 | 235.54 | <0.001 |
| Seed weight | 0.52 | 2 | 12.47 | <0.001 |
| Burial depth × seed weight | 1.02 | 10 | 4.88 | <0.001 |
| Residual | 1.12 | 54 | | |

both temperature conditions (Table 1) and had no influence on the germination rate of this *A. artemisiifolia* population (Table 1).

### Effects of the burial depth and seed weight on germination and emergence

The germination and seedling emergence of the Pluvet population were significantly influenced by the burial depth and seed weight (Table 2). Significant effects of interactions (burial depth × seed weight) also were detected. No germination and no seedling emergence were observed for the seeds that were buried deeper than 8 cm (Fig. 2). The germination of the seeds that were placed on the surface (0 cm) was comparable to the germination results that were obtained in the Petri dishes (*t*-test: $F = 2.492$, $P = 0.287$). The level of seedling emergence was similar to the germination results for the seeds that were placed on the surface (0 cm) (Fig. 2). The 2 cm burying of the seeds did not alter the germination and seedling emergence (Fig. 2). For the seeds that were placed 4 and 8 cm deep, the germination and emergence were significantly reduced, compared with those that were buried at the more superficial depths (Fig. 2). When the seeds were at the soil surface, the seed weight had no influence on germination and seedling emergence (Fig. 2). The seed weight modified the germination for the seeds that were placed 2, 4, and 8 cm deep: the L seeds germinated less well than those of the two other classes (Fig. 2a). The seedlings from only the H seeds emerged from the 8 cm depth (Fig. 2b). Although at least 46.2% of the seeds were able to germinate at this depth, only 4.9% of the seedlings were able to emerge.

## DISCUSSION

The majority of the seeds that were produced was viable and was able to germinate as soon as the environmental

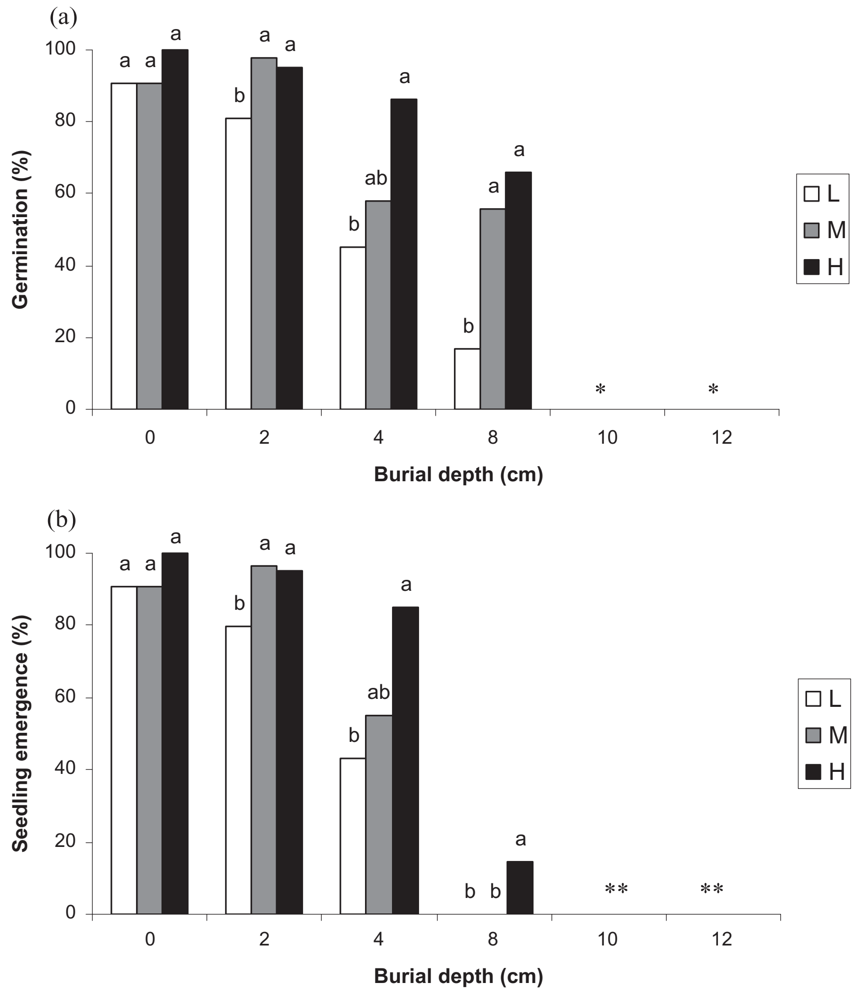


**Fig. 2.** (a) Germination and (b) seedling emergence of *Ambrosia artemisiifolia* seeds of the Pluvet (2005) population for three weight classes (light [L], medium [M], and heavy [H]) at several burial depths. For each depth, the bars with different letters are significantly different at $P < 0.05$. *, no germination; **, no emergence.

conditions were favorable after the removal of primary dormancy. When the temperature was less favorable, the germination level was significantly reduced. However, the germination percentages of these seeds were high, with a minimum value of 76.8%. This attests to the high reproductive success of these various experimental populations of *A. artemisiifolia*, in comparison with other allogamous weeds, such as *Alopecurus myosuroides* Huds. (Moss 1990). The seed weight had no influence on the seed germination of *A. artemisiifolia*, as in the case of other Asteraceae species (e.g. *Centaurea eriophora* L.) (Ruiz de Clavijo 2002) and as in the case of species of other botanical families, such as *Dactylis glomerata* L. (Bretagnolle *et al.* 1995) and *Andropogon tectorum* Schumach. (Smith 1998). However, it has been observed that the germination of heavier seeds is higher for several species, such as *Lithospermum arvense* L. (Milberg *et al.* 1996) and *Abutilon theophrasti* Medik. (Baloch *et al.* 2001), but lower for other species, including *Erodium brachycarpum* (Godron) Thell. (Stamp 1990). This effect depends on the species: the germination percentage can increase, decrease, or remain unaffected by different seed sizes (Baskin & Baskin 1998). Thus, generalizations about the effect of the seed weight on germination are difficult to establish.

The variable seed size of *A. artemisiifolia* is a strategy that could allow this weed species to cope with the highly variable environmental conditions that are found in ruderal habitats or in fields. Heavy-sized seeds could enable *A. artemisiifolia* to produce competitive plants and light-sized seeds could allow it to persist in the soil and to wait for favorable conditions to germinate (Harper *et al.* 1970; Fumanal *et al.* 2007).

The seed weight did not influence the germination rate of *A. artemisiifolia*. However, Tungate *et al.* (2002) observed the opposite phenomenon in another species: the light seeds of *Senna obtusifolia* (L.) H.S. Irwin & Barneby germinated faster than the heavy seeds. As in the case of the germination percentage, the germination rate depends on the species. In all cases, the germination rate could influence seedling emergence. A rapid germination rate allows earlier seedling emergence, which confers advantages on plants: a prolonged growth period without competition and a competitive advantage over other plants (Washitani & Nishiyama 1992).

Seed burial also could influence the demography of *A. artemisiifolia*. As the burial depth for *A. artemisiifolia* increased, both the germination and seedling emergence declined. Germination and emergence after burial also depend on the seed weight and a decrease in emergence due to an increased burial depth has been reported for several other weeds (Benvenuti *et al.* 2001). As in the case of *Ambrosia trifida* L. (Harrison *et al.* 2007), there was no difference in the germination and emergence with the seed size when the *A. artemisiifolia* seeds were deposited on the soil surface. The germination and emergence of the light seeds of *A. artemisiifolia* were significantly reduced as soon as the seeds were buried at a 2 cm depth. Heavier seeds might be favorable in habitats where seeds are buried. Heavier seeds with higher energy reserves could emerge from greater burial depths (Thomas *et al.* 2006; Harrison *et al.* 2007). The soil's characteristics, water-holding capacity, and gas environment conditions at different depths could explain the variations in germination and emergence (Benvenuti & Macchia 1995). In the current experiment, a 10 cm depth was found to be the limiting depth for the germination and emergence of *A. artemisiifolia*. However, Martinez *et al.* (2002) obtained no emergence at an 8 cm depth for *A. artemisiifolia*, but the soil was composed only of sand. This soil effect is in contradiction with the results that were obtained by Ghorbani *et al.* (1999) and Benvenuti (2003) for the species, *Amaranthus retroflexus* L. and *Datura stramonium* L., respectively. Indeed, the level of emergence in sandy soil was generally greater than that in clay soil. The reduction of germination that was observed in the clay soil with an increasing burial depth should be linked largely with poor gas exchange in the environment of the buried seeds (an increased risk of hypoxia and accumulation of germination-inhibiting metabolites) (Benvenuti 2003). The results that were obtained for *A. artemisiifolia* showed that it was not always the same soil properties that influenced the germination of the buried seeds.

At the 10 cm depth, *A. artemisiifolia* was not able to germinate or emerge, which confirmed the results that were obtained by Stoller and Wax (1973). For giant ragweed (*A. trifida*), emergence was obtained for the seeds that were buried down to 16 cm (Abul-Fatih & Bazzaz 1979). This difference can be explained by the seed size: the seeds of *A. trifida* (>6 mm long) are larger than those of *A. artemisiifolia* (2–3.5 mm long). As Gebben (1965) found, a greater level of germination and emergence of *A. artemisiifolia* was obtained for the seeds on the soil surface, in comparison with those that were buried. However, for many species, the seeds on the soil surface have a lower level of emergence, compared to the seeds that are placed in the first upper centimeters of soil (Boyd & Van Acker 2003). In this case, lower emergence on the soil surface probably is related to the discontinuous or lower availability of moisture or to limited soil-to-seed contact (Ghorbani *et al.* 1999). For *A. artemisiifolia*, the greatest seedling emergence occurred for the seeds that were placed on or near the soil surface, which could explain why this species is partly associated with areas, such as roadsides or abandoned agricultural fields, and also suggests that no-till or reduced tillage practices could promote seedling emergence in the field. The use of the stale seedbed technique during non-cultivation periods would reduce the amount of seeds that exist on or near the soil surface. Moreover, a moldboard plow, which buries seeds to below 10 cm, could be efficient in decreasing the success of this species, but only if future soil tillage is carried out at shallower depths. Thus, this plant is characterized by a long-term, persisting seed bank (Basset & Crompton 1975). These suggestions should be tested in field experiments.

In conclusion, *A. artemisiifolia* has become an invasive plant in France (Chauvel *et al.* 2006). The high capacity of the seeds to germinate and to emerge on the soil surface and seed persistence in the soil seed bank (Toole & Brown 1946) must be the principal factors that explain the success of *A. artemisiifolia* in fields and uncultivated areas.

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