Susceptibility of the Early Growth Stages of Volunteer Oilseed Rape to Invertebrate Predation

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Abstract

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Chemical and agronomical control of volunteer plants is difficult, especially in reduced-input cropping systems where feeding by natural herbivores may become an important cause of their mortality. The consumption of the early growth stages of winter oilseed rape (*Brassica napus* L. ssp. *napus*) by five species of ground-surface invertebrates abundant in rape fields of Central Europe was studied under laboratory conditions. The species were particular in their preferences for growth stages of oilseed rape. The gastropods *Arion lusitanicus* and *Helix pomatia* preferred seedlings rather than seeds, whereas all three species of arthropods rejected seedlings. *Pseudoophonus rufipes* consumed all seed stages with similar intensity, while *Pterostichus melanarius* readily accepted fresh, dry and imbibed seeds. The overall consumption by the isopod *Armadillidium vulgare* was low and concentrated on exhumed seeds. Seeds and the early growth stages of oilseed rape are thus susceptible to invertebrate predation, each stage being killed by a specific group of invertebrate predators.

Keywords: volunteer seeds; seed and seedling mortality; carabid beetles; gastropods; terrestrial isopods

Oilseed rape (*Brassica napus* L. ssp. *napus*) is the most important of the oilseed crops of temperate zones (Diepenbrock 2000), and it is mostly grown for the vegetable oil that is used for human consumption or biofuel production (Alford 2003; Stephenson *et al.* 2008). The area under oilseed rape recently increased across the European Union (Diekotter *et al.* 2010) and other countries (Faostat 2010). However, oilseed rape farming has inherent serious environmental and agronomical risks. An important problem is the emergence of strong volunteer populations, originating from the extensive seed shattering that occurs before or during harvest (Schlink 1998; Gruber *et al.* 2004; Warwick & Stewart 2005; Beckie & Warwick 2010). Seeds fall onto the ground where they germinate, or they become buried in the soil where they form a long-persisting seed bank (Lutman 1993; Begg *et al.* 2006), which is ready for germination whenever exhumed. The problem of volunteerism thus becomes more serious if oilseed rape is grown in monoculture. Besides the technological innovations that would reduce seed shatter, an enhanced mortality of the fallen seeds is a way of reducing the risks of the establishment of volunteer rape populations.

The post-dispersal mortality of seeds is an important factor of plant life; the mortality that a plant species may suffer during the period between seed dispersal and seedling establishment is enormous (Vander Wall *et al.* 2005; Kauffman & Maron 2006; Harper 2010). This mortality has various causes, including failed germination, physiological death, diseases and predation (Booth *et al.* 2003). Recently, Honek *et al.* (2009) demonstrated that for the establishment of dandelion (*Taraxacum* agg.), several groups of invertebrates, carabids, isopods and gastropods are specific for the consumption of particular stages of a young plant, and

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as a result, complement each other in their impact on the overall mortality. In that particular study, carabids were the major predators of seeds, while gastropods depleted the populations of seedlings. Moreover, Martinková *et al.* (2006) demonstrated that weed seeds exhumed from the soil bank and fresh seeds of the same species may differ in their susceptibility to ground beetle predation.

Both field and laboratory data provide evidence that rape seeds are subjected to predation (Gruber & Claupein 2006; Koprdová *et al.* 2008; Saska 2008a), but the variation in predation rates of sentinel seeds exposed on the ground is enormous (0–100%) and depends on the year, season and site of exposition (Saska 2008a). As the crop matures and is harvested, various quantities of seeds are shattered, which sometimes literally inundates the soil surface (Lutman 1993). Depending on the weather, the seeds either germinate quickly (Pekrun *et al.* 1997), leaving only a short-time window for predation or, under dry conditions, the period available for predation may extend until soil tillage (Lopéz-Granados & Lutman 1998). However, germinated seeds and young seedlings do not escape from predation and may also be eaten by invertebrates (Honek *et al.* 2009), a fact which has not yet been well documented for many plants. In the case of oilseed rape, gastropods are known to graze on seedlings intensively (Moens & Glen 2002). Moreover, because of a persistent soil bank (Lutman 1993; Begg *et al.* 2006), ploughing may bring to the surface viable seeds that replace the freshly shattered ones. The palatability and consumption rates of exhumed seeds also remain to be studied.

Our preliminary knowledge of the predation of weed and rape seeds and seedlings (Koprdová *et al.* 2008; Saska 2008a; Honek *et al.* 2009) determined the selection of rape developmental stages and the consumers that were investigated in this study. We selected five early growth stages of winter rape, fresh, exhumed, imbibed, and germinating seeds and early seedling, and presented them to five species of invertebrates (one species of terrestrial isopods, two species of carabid beetles and two species of gastropods) that are frequently encountered in the fields of oilseed rape in the Czech Republic and are known to consume seeds and/or seedlings. Rape mortality was then recorded under standard laboratory conditions. We were interested in differences in the susceptibility of rape growth stages to predation and in the specificity of the predator species in consuming a particular stage.

MATERIAL AND METHODS

Invertebrates. The susceptibility of early growth stages of winter oilseed rape (*Brassica napus* L. ssp. *napus*) to ground-dwelling invertebrates was tested using species selected according to previous laboratory studies (Koprdová *et al.* 2008; Saska 2008a) and field observations (P. Saska, pers. obs.). The species included were *Pterostichus melanarius* (Illiger) [average dry body mass: 46 mg] (Coleoptera: Carabidae), *Pseudoophonus rufipes* (DeGeer) [31 mg] (Coleoptera: Carabidae), *Armadillidium vulgare* Latreille [18 mg] (Isopoda: Armadillidiidae), *Arion lusitanicus* (Mabille) [631 mg] (Gastropoda: Arionidae) and *Helix pomatia* Linnaeus [1866 mg, shell excluded] (Gastropoda: Helicidae).

Carabids and *A. vulgare* were collected in Prague-Ruzyne, Czech Republic (50°06'N, 14°15'E) in July and August of 2008, using standard pitfall traps (Saska 2008a) that consisted of 300 ml plastic cups, 7.5 cm in diameter, 12 cm deep, which were placed with the rims at the ground level and covered with a metal roof to avoid flooding. Gastropods were collected by hand in the same area in May and June of 2009. To standardise the level of satiation, all specimens were starved for 3 days at 5°C and were kept in plastic cups and containers with moist filter paper.

Oilseed rape. The oilseed rape seeds originated from crops grown in Prague-Ruzyně and were harvested on two dates and stored as follows: those harvested in July of 2007 were stored under room conditions until the experiment (growth stages [i] and [iii–v]); and those harvested in July of 2006 were stored under room conditions until October 10, wrapped into a nylon bag and buried at a 20 cm depth under grass, then exhumed on April 10, 2007, and stored under room conditions until the experiment (growth stages [ii]). The experimental seeds used were dry, imbibed or germinated to early developmental stages and treated as shown in Table 1. The growth stages of oilseed rape (Lancashire *et al.* 1991) used in the experiment were the following:

[i] BBCH 00 – dry seed laboratory stored (referred to as "fresh")
[ii] BBCH 00 – dry seed exhumed
[iii] BBCH 03 – seed imbibition complete
[iv] BBCH 08 – hypocotyl with cotyledons growing towards the soil surface
[v] BBCH 10 – cotyledons completely unfolded

Table 1. A protocol for the preparation of oilseed rape early growth stages for consumption experiments

Stage	Preparation
[i] BBCH 00	seeds used from dry storage bag
[ii] BBCH 00	exhumed seed used from dry storage bag
[iii] BBCH 03	seed from dry storage bag imbibed for 2 days on moist filter paper (Petri dish, 200 mm) at 25°C
[iv] BBCH 08	seed from dry storage bag imbibed for 3 days on moist filter paper (Petri dish, 200 mm) at 25°C
[v] BBCH 10	seed from dry storage bag sown on a 10-mm layer of moistened garden soil (Petri dish, 200 mm) and germinated for 4–5 days at 25°C

Consumption experiments. The consumption of rape developmental stages was monitored in plastic containers (19 cm in diameter, 6.5 cm deep for *H. pomatia*) or plastic cups (8 cm in diameter, 5 cm deep for other species) that were sealed with a perforated plastic lid. Experimental vials were filled to a depth of 2 cm with sieved garden soil. Twenty rape individuals of a particular growth phase were transferred from their storage paper bag (stage [i] and [ii]) or incubation vial (stage [iii] and [iv]) to each experimental vial and placed on top of the soil. Individuals of stage [v] were transferred together with a bulk of soil in which they germinated to prevent root damage.

A single individual of one of the invertebrate species was introduced to each experimental vial and kept in the laboratory at a mean temperature of 21°C and a natural photoperiod. Rape seeds or seedlings were exposed to predation for one day in 10 replications per growth stage. The number of seeds or seedlings remaining per dish (not eaten) was then counted. Seeds that had more than a half of their volume eaten, and seedlings both cotyledons of which were consumed, were considered eaten.

Statistical analysis. Statistical analysis was performed using the statistical package R, Version 2.8.1 (Venables *et al.* 2008). With respect to the predator species, we evaluated interspecific variation in (*i*) individual consumption and (*ii*) specific consumption recalculated per unit body mass. Due to differences in body size among the species of predators, the consumption values were standardized prior to the analysis of interspecific differences. Individual consumption was first standardized to the proportion of maximum consumption within each species of predator (Honek *et al.* 2007) ranging from 0 (zero predation) to 1 (maximum predation), which removed the confounding effect of the predator size on consumption. Interspecific differences were then tested by ANOVA on standardized differences, using the predator species and growth stage as factors and including their interactions.

Intraspecific differences in consumption were analysed on raw consumption data, using the analysis of deviance with Poisson errors and log-link functions for each species of predator separately and designating the growth stage as single factor. If needed, the quasi-distribution with the log-link and variance increasing with the square of the mean was applied to control for overdispersion and improve the structure of errors (Crawley 2005). If the main effect of the growth stage was significant, the analysis proceeded with collapsing insignificant factor levels to achieve the minimum model containing only significantly different terms (Crawley 2005). When absolutely rejected by the predator, the stage of the seedling [v] was excluded from the analysis due to a zero variance.

RESULTS

The individual consumption of rape seeds or seedlings varied with the invertebrate species and rape developmental stage (Figure 1). The average daily consumption of the plant growth stage that was most eaten by each of the species decreased with the body size of the consumer, being highest in *H. pomatia* (stage [v]: 19.3 ± 0.35 rape individuals), followed by *A. lusitanicus* ([iv]: 17.7 ± 0.45), *P. rufipes* ([ii]: 12.7 ± 1.74), *P. melanarius* ([i]: 6.5 ± 1.11) and *A. vulgare* ([iv]: 2.5 ± 0.67). The preferences of each particular species of consumer differed; the major difference was that gastropods readily consumed young seedlings (stage [v]), while arthropods did not eat this stage at all. The standardized consumption of rape at different growth stages significantly varied among the species of predator (ANOVA: $F_{24,225} = 21.530$, $P < 0.001$; Table 2). All terms of the maximum model were significant (Table 2), which indicated that the predators were specific in their preferences for a growth stage (Figure 1).

The consumption of the earlier growth stages ([i]–[iv]) varied with the consumer species. In *H. po-*

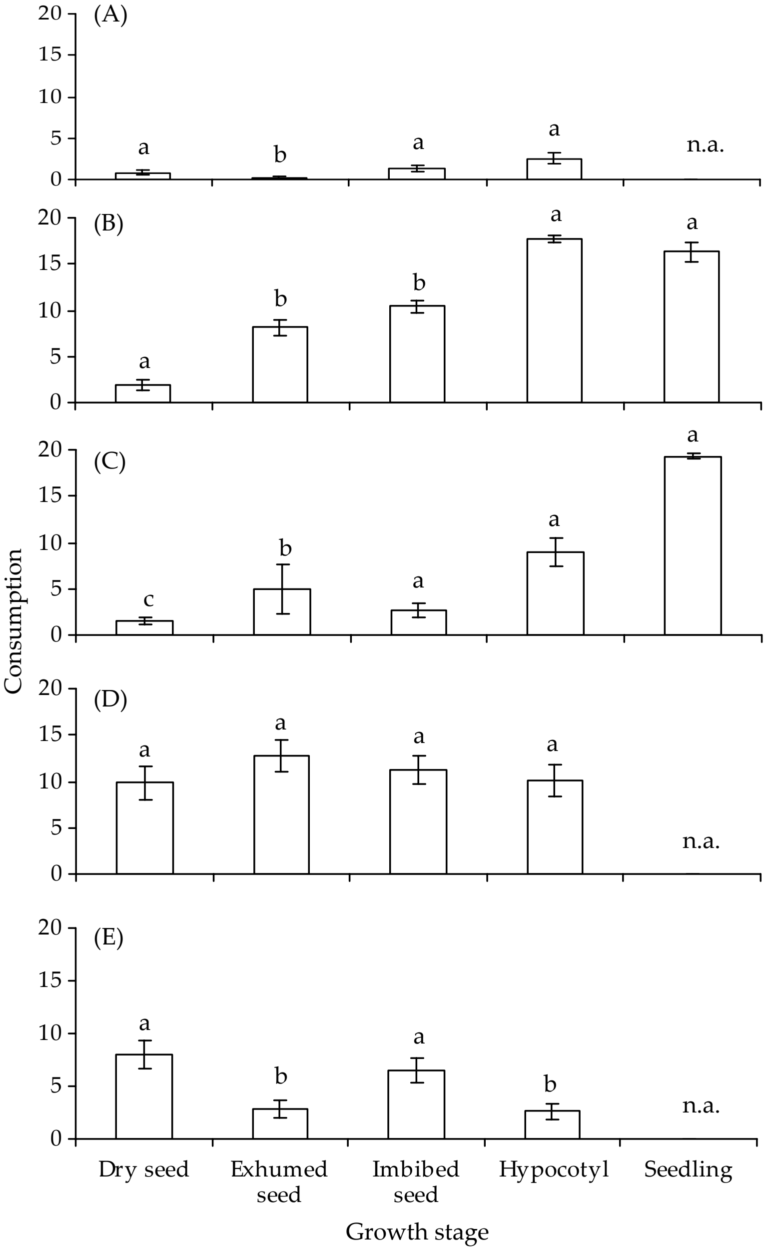

Figure 1. The consumption (mean ± SE) of the growth stages of oilseed rape by five species of invertebrates: (A) *A. vulgare*; (B) *A. lusitanicus*; (C) *H. pomatia*; (D) *P. rufipes*; (E) *P. melanarius*

The same letters within each species of predator indicate groups of stages combined according to the minimum model. n.a. – excluded from the analysis due to zero variance

matia, consumption increased with advancing rape development; in other species there was either a loose parallel between increasing consumption and progressing plant development (*A. lusitanicus, A. vulgare*) or the variation displayed no trend (*P. rufipes, P. melanarius*). The preferences of predators to growth stages were confirmed in separate analyses, using the raw consumption values (Table 3). Both species of gastropods accepted all growth stages of winter rape (Figure 1). Although the minimum model for *A. lusitanicus* differed from that of *H. pomatia*, the overall trend was similar; both species of gastropods tended to consume seedlings rather than seeds, with the least consumed stage being dry seeds (Figure 1). All three species of arthropods completely rejected seedlings (Figure 1). The omnivorous carabid, *P. fipes*, consumed the other four growth stages of winter rape equally (Table 3 and Figure 1), while the 'carnivorous' *P. melanarius* preferred dry and imbibed seeds in favour of exhumed and germinating ones

Table 2. Differences in the standardised consumption of different stages of rape seeds and seedlings

Term	DF	*F*	*P*
Species of predator	4	35.331	<< 0.001
Seed stage	4	9.728	<< 0.001
Species of predator × seed state	16	21.023	<< 0.001
Residuals	225		

Table 3. Analysis of deviance on the consumption of different growth stages of winter rape by five species of invertebrates

Species	Error structure	Full model			Minimum model			Deletion test‡
		DF	deviance	*P*	DF	deviance	*P*	*P*
A. lusitanicus	p	4	180.554	<< 0.001	2	177.110	<< 0.001	0.179
H. pomatia	q	4	34.556	<< 0.001	2	32.730	<< 0.001	0.390
A. vulgare	q	3†	8.883	0.031	1	7.200	0.007	0.808
P. rufipes	q	3†	0.656	0.512				
P. melanarius	q	3†	9.360	< 0.001	1	9.303	<< 0.001	0.951

p – Poisson distribution; q – quasi distribution with log-link and variance increasing with the square of the mean; ‡maximum vs. minimum model; †seedling stage with zero variance was excluded from the analysis

(Table 3 and Figure 1). Overall, the rape consumption by *A. vulgare* was low (Figure 1), being significantly the lowest in the case of exhumed seeds, compared to other treatments (Table 3 and Figure 1).

DISCUSSION

This paper concerns the susceptibility of the early growth stages of rape to predation by invertebrates. The five species of invertebrates used in this study were reported as predators of seed and/or seedling oilseed rape (Frank 1998; Chevalier *et al.* 2003; Koprdová et al. 2008; Honek *et al.* 2009; Kozlowski & Kozlowska 2009). This study discriminates the predation between particular phenological phases of oilseed rape in a parallel experiment for the first time.

We found that all growth stages were susceptible to predation, but there were noticeable preferences among the different species of predators for particular growth stages of oilseed rape. The carabids were very efficient predators of all developmental stages, except seedlings; seeds exhumed from the soil bank were also accepted. *Pseudophonus rufipes* ate 10–12 seeds per day and was less selective in its preferences for particular developmental stages than *Pterostichus melanarius*, which are 2–8 seeds per day. This correlates with different feeding habits of the two species. *P. rufipes* is a generalist predator (Holland 2002) that has a diet that includes many species of seeds (Honek *et al.* 2003, 2007). In contrast, *P. melanarius* is well known as a carnivorous predator of pest insects (Holland 2002), which will reluctantly eat small species of weed seeds in the absence of choice (Honek *et al.* 2003). The massive consumption of oilseed rape seeds was first observed by Koprdová *et al.* (2008), also in an experiment that provided 'no choice' to the predator. In our experiment, *P. melanarius* preferred dry and imbibed seeds, probably because they are more nutritious than exhumed or germinated seeds in which the oil content may be changed (exhumed seeds) or metabolised (germinated seeds). We propose that the carnivorous *P. melanarius* switches to seeds before the rape harvest, when seeds are shed onto the ground in large quantities; easy-to-handle seeds might dominate its food budget and replace animal prey in that period of the year. Consequently, mismatch between temporal curves of seed predation and activity-density of granivorous carabids in the study of Saska (2008a) may have been partly caused by not including this carabid species.

Gastropods were specific predators of seedlings, which were consumed in quantities of up to 20 seedlings per day, and these data support previous findings (Moens & Glen 2002). The earlier growth stages of winter rape were also accepted, more by *Arion lusitanicus* than by *Helix pomatia*. *A. lusitanicus* was the dominant predator of germinating seeds ([iv]), eating approximately 18 seeds per day. The small seeds of dandelion (*Taraxacum* agg.) may pass through the gut of *A. lusitanicus* and remain able to germinate after defecation (Honek *et al.* 2009); whether dry and imbibed rape seeds survive digestion by gastropods is not known. We suggest that germinating seeds probably lose viability after being consumed because of mechanical destruction or enzymatic violation of the root or hypocotyl. Gastropod preference to seedlings is in agreement with the field observations – locally they can be serious pests in establishing oilseed rape cultures (Moens & Glen 2002). While cultural rape needs to be chemically protected against gastropods in some countries (Moens & Glen 2002), their presence in stands of volunteer oilseed rape stands might be regarded as beneficial, due to their preference for this plant (Briner & Frank 1998).

The terrestrial isopod, *Armadillidium vulgare*, was a weak predator of winter rape seeds and seedlings, probably because of its small size. Terrestrial isopods consume small species of seeds and seedlings (Saska 2008b; Honek *et al.* 2009), whereas a large seed size is a deterrent of consumption (Saska 2008b).

The consumption of the early developmental stages of rape was demonstrated by all of the investigated species of predators, which may be beneficial for the biological control of volunteerism. Carabids and gastropods attack seeds efficiently, destroying the cotyledons, young roots and hypocotyl; once the seedlings have emerged, they can be grazed by gastropods as well. Additionally, seeds that enter a long-persisting soil seed bank (Lutman 1993) may eventually get back to the surface (e.g. by cultivation), where they can be destroyed by carabid beetles.

How important is the predation by the above species in the biological control of oilseed rape volunteerism? Actual predation in the field depends on factors including predator numbers, the presence of alternative foods and duration of seed and seedling exposure (Lundgren 2009). The activity of seed-eating carabids may cover the entire field, but they are usually unevenly distributed in patches (Thomas *et al.* 2000; Holland *et al.* 2005; Saska *et al.* 2007). The presence of an alternative food source might detract from seed consumption by carabids (Lundgren 2009). Molluscs abundantly inhabit crop margins (Frank 1998); they only reluctantly disperse into the central parts of the fields (Honek & Martinková 2011). Oilseed rape is, however, their preferred food plant (Brinner & Frank 1998) and the weed species that might provide an alternative food are scarce in well-developed stands with a dense crop canopy. Under conditions that allow germination, the shed seeds are usually exposed to predation for a short period, which does not provide enough time to predators to act efficiently. The real importance of natural predation on early oilseed rape stages for the control of volunteerism probably varies in place and time, as indicated by Saska (2008a), but remains to be properly estimated.

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