



Pronounced effects of slug herbivory on seedling recruitment of *Brassica* cultivars and accessions, especially those with low levels of aliphatic glucosinolates

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Abstract

In demographic studies on *Brassica* cultivars and accessions we observed large genotypic variation in the ability of seedlings to establish. Here we quantify the role of slugs during establishment by including and excluding slug herbivory.

Slug exclusion during the first 10 days after germination led to 26.5 times more surviving seedlings in modern canola varieties of *Brassica napus*, 4.3 times more in feral *B. napus* and 1.9 times more in wild *Brassica rapa*. While seed and seedlings of canola were low in aliphatic glucosinolates (AGS), feral *B. napus* and wild *B. rapa* had much higher AGS levels. Consequently, we find a positive correlation between the survival of young seedlings and AGS concentration. Concentrations of indole glucosinolates (IGS) in seeds were much lower than those of AGS and did not correlate significantly with survival. Subsequently, we exposed 10-day-old seedlings to herbivory. In the 4 days following exposure, slug herbivory was negatively correlated to AGS concentration but not to IGS.

In choice experiments in the lab, the preference of the slug *Arion lusitanicus* also correlated negatively with AGS content. *A. lusitanicus* preferred to feed on *B. napus* rather than on wild *B. rapa*, but had no significant preference when presented with plants similar in AGS content.

Slugs can be a limiting factor for seedling recruitment in populations of *B. napus*, especially for modern canola cultivars with a low AGS content.

Zusammenfassung

In demographischen Studien mit kultivierten und verwilderten Formen von *Brassica napus* und wilden *Brassica rapa* beobachteten wir große genotypische Variabilität in der Etablierung von Sämlingen. Hierzu quantifizierten wir die Rolle von Schnecken während der Etablierung von Sämlingen durch experimentellen Ein- oder Ausschluß von Schnecken.

Der Ausschluß der Schnecken während der ersten 10 Tage nach der Keimung führte zu 26,5 mal mehr überlebenden Sämlingen in modernen Canola-Varietäten von *B. napus*, 4,3 mal mehr in verwilderten *B. napus* und 1,9 mal mehr in wilden *B. rapa*.

Keywords: *Arion lusitanicus*; *Brassica napus*; *Brassica rapa*; Canola; Indole glucosinolates

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Samen von Canola-Varietäten wiesen eine niedrige Konzentration von aliphatischen Glucosinolaten (AGS) auf, die von verwilderten *B. napus* und *B. rapa* eine wesentlich höhere. Dementsprechend fanden wir eine positive Korrelation zwischen AGS-Konzentration und dem Überleben von jungen Sämlingen. Es gab keine signifikanten Korrelationen zwischen indol-Glucosinolaten (IGS) und dem Überleben von Sämlingen.

In einem weiteren Experiment wurden 10 Tage alte Sämlinge den Schnecken zum Fraß angeboten. Während der ersten 4 Tage nach dem Einsetzen der Schnecken litten die Sämlinge mit niedrigem AGS wieder mehr unter Fraß. Die Konzentrationen von IGS waren in den Samen bedeutend niedriger als jene für AGS und korrelierten nicht mit der Fraßrate. In Wahlexperimenten im Labor war die Präferenz der Schnecke *Arion lusitanicus* negativ korreliert mit der AGS-Konzentration. *A. lusitanicus* bevorzugte *B. napus* über *B. rapa*, aber zeigte keine signifikante Präferenz, wenn sie die Wahl hatte zwischen Varietäten mit gleicher AGS-Konzentration.

Schnecken sind ein limitierender Faktor für die Rekrutierung von Sämlingen, insbesondere für moderne Canola-Varietäten mit niedrigen AGS-Konzentrationen.

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Introduction

High mortality in the seed and seedling stages can substantially affect the population dynamics of plants (Harper 1977; Honek, Martinkova, Saska, & Koprdova, 2009; Koprdova, Saska, Honek, & Martinkova 2012; Honek, Saska, Martinkova, & Koprdova, 2013). Predation can strongly reduce seed numbers (Louda 1982; Fenner & Thompson 2005; Honek, Martinkova, & Saska, 2005). Across all species studied in the BIOSIS database between 1969 and 2002, herbivory was the most important reason for mortality in seedlings (Moles & Westoby 2004). Some studies indicated effects of selective herbivory on the composition of plant populations (Hulme 1996; Elger, Lemoine, Fenner, & Hanley 2009; Hanley & Sykes 2009). Relatively few papers emphasized that slugs, although often considered generalist herbivores, can be highly selective and could potentially have large effects on seedling recruitment of some species in the plant community (Buschmann, Keller, Porret, Dietz, & Edwards 2005; Strauss et al. 2009). Falk et al. (2014) found for *Arabidopsis thaliana* that mucus of slugs triggered the jasmonate pathway, so that this plant species employs induced defence against slugs.

In a demographic study in the Netherlands, Hesse and de Jong (2014, in preparation) found large differences in seedling survival between many *Brassica* lines. After ploughing a field and removing all vegetation, they sowed seeds of several *Brassica napus* L. (oil seed rape) cultivars, of feral *B. napus* collected in roadside populations and of wild *Brassica rapa* L. Seedlings of all groups survived well in the first year, with no apparent signs of herbivory. Seed production in the first year was high for all cultivars and accessions and the fraction seed predation in the fruit was similar for all lines. In the next year, however, when the vegetation cover had increased, very few seedlings of modern *B. napus* cultivars survived and their populations became extinct. This contrasted with the wild *B. rapa* accessions that did manage to establish in the second year. The *B. napus* crop has bigger seeds than the wild *B. rapa* and, contrary to field observations, one would expect these big seeds to be more competitive and to

establish better in the presence of vegetation. Slugs were apparent in the field plots, but at that time no further quantification was made of their effects. The above findings suggest that seed and seedling characteristics can be major factors influencing survival rate. Certain aliphatic glucosinolates (AGS), especially progoitrin, are detrimental for human and animal health (Fahey, Zalcmann, & Talalay, 2001) and plant breeders have therefore selected for very low AGS levels in the seeds of the crop *B. napus*. They have also selected against the presence of erucic acid in the seeds. Modern canola cultivars are ‘double-zero’: seeds have low levels of both AGS and erucic acid. Several authors have emphasized the role of GS as an anti-herbivore defence in the *Brassicaceae* (Giamoustaris & Mithen 1995; Fahey, Zalcmann, & Talalay 2001; Wittstock & Halkier 2002). However, the overall effect of GS is far from clear. Some authors have indicated that generalist herbivores, especially birds and slugs, are deterred, while specialist insects are unaffected or even stimulated by high GS concentrations (Giamoustaris & Mithen 1995; Bodnaryk 1997; Hopkins, van Dam, & van Loon 2009). The composition of the GS changes as the plant grows and the function of this change is also not well understood. For instance, in *Arabidopsis thaliana* indole GS (IGS) are major constituents of leaves, especially when they age, while AGS are present in very high concentrations in seeds (Brown, Tokuhisa, Reichelt, & Gershenzon 2003). Falk et al. (2014) emphasized that high concentrations of AGS deter feeding of the slug *Arion lusitanicus* on *A. thaliana*, while *Helix pomatia* may even be more sensitive to GS.

The role of slug damage on *B. napus* has received attention in an agricultural context (Glen, Jones, & Fieldsend, 1990; Frank & Friedli 1999). In no-choice experiments the Spanish slug *A. lusitanicus* ate more from *B. napus* than from most other plant species (Briner & Frank 1998; Kozłowski & Kozłowska 2009). Kozłowski and Kozłowska (2004) reported that three different slug species all ate more *B. napus* than twenty other plant species from different families. Briner and Frank (1998) used the double-zero cultivar Express (T. Frank, personal communication, 2014), Kozłowski and Kozłowska (2004) the low-GS cultivar Kana (J. Kozłowski,

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