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Slug herbivory on hybrids of the crop *Brassica napus* and its wild relative *B. rapa*

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Abstract

Some plant species can cross with each other but stay nevertheless distinct with little gene flow between them. Selective herbivory could explain this pattern when hybrids are more susceptible or intermediate between their parents. We performed choice and no-choice experiments with the slug *Arion lusitanicus* to test this hypothesis for the crop *Brassica napus*, wild *B. rapa* and their backcross hybrids. In both experiments slugs greatly preferred *B. napus* over *B. rapa* while average herbivory on backcross hybrids was intermediate. Concentrations of aliphatic glucosinolates in the hybrids were intermediate between the parental species. Slug herbivory potentially reduces establishment of backcross hybrids. This hypothesis needs to be tested in the field.

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Introduction

Crossing related plant species often generates hybrid seeds that are able to germinate and grow well in the lab. Yet apparently some mechanism keeps the species distinct in the field (Stace 1975). Hybrids may not be formed in the field when the parent species are separated in time or space or when pollination relies on different flower visitors or pollination mechanisms. Alternatively, viable hybrids are formed but are not fit to survive under field conditions due to adverse

selective forces from abiotic conditions, competitive interactions with other plants or interactions with antagonists such as pathogens, seed predators or herbivores.

Research on the defence of hybrids started with the discovery that hybrid zones support high densities of herbivores (Floate, Kearsly, & Whitham 1993). These authors hypothesized that the hybrid was more susceptible to herbivory than each of its parents (hybrid susceptibility hypothesis). Fritz, Nichols-Orians, and Brunsfeld (1994) mentioned three alternatives. The effects of the defence traits may be additive and hybrids are intermediate between their parents in herbivory (additive hypothesis). When defence traits are dominant, hybrids have the same low level of herbivory as the best-defended parent (dominance hypothesis). Finally, hybrids could also be more resistant than their parents (hybrid resistance hypothesis). The data of Fritz et al. (1994) best sup-

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ported the hybrid susceptibility hypothesis, but all patterns occur in nature (Fritz, Mouliia, & Newcombe 1999). In studies on gastropods the susceptibility hypothesis was confirmed for the slug *Arion fuscus* feeding on *Senecio* hybrids, while herbivory of a snail species (*Trochulus striolatus danubialis*) on the same hybrids was intermediate, supporting the additive hypothesis (Bog et al. 2017). The hybrid resistance hypothesis applied to the invasive slug (*Arion subfuscus*) feeding on willow hybrids (Orians, Fritz, Hochwender, Albrechtsen, & Csezak 2013). For gene flow between species both the performance of the F₁ and of the later-generation hybrids is relevant. When the first generation performs well but later generations fail, no introgression will occur. Resistance of later-generation hybrids to fungal pathogens was in most cases intermediate between the parents in *Populus*, confirming the additive hypothesis (LeBoldus, Isabel, Floate, Blenis, & Thomas 2013).

The Korean–Japanese botanist U (1935) elucidated the relationships between different *Brassica* species. *Brassica rapa* (AA genome, $2n=20$) is a common wild species in Western Europe, occupying disturbed road- and watersides. *B. rapa* is self-incompatible and fully outcrossing. *Brassica napus* (oil seed rape) is a common, self-pollinating crop in Europe and North America. *B. napus* is an allotetraploid and has the AACC genome (U 1935) with $2n=38$. Molecular data indicate a recent origin of this crop species (Chalhoub et al. 2014). The AA in *B. napus* is derived from *B. rapa* and the CC from the cabbage (*B. oleracea*) genome with $2n=18$. No stable natural populations exist of *B. napus* but with repeated input of seeds the species can persist in feral populations due to a long-lived seed bank in the soil (Luijten & de Jong 2010; Belter 2016; Franzaring et al. 2016). Crosses between *B. rapa* and *B. napus* can easily be made by hand so there is potential for gene flow from the crop to the wild species. Bees have been observed to move between flowers of *B. rapa* and *B. napus* in the field (Ronca, Allainguillaume, Ford, Warren, & Wilkinson 2017; de Jong personal observation 2017). F₁ hybrids with the AAC genome have been identified in the field in the UK (Wilkinson et al. 2000; Allainguillaume et al. 2006) and the Netherlands (Luijten, Schidlo, Meirmans, & de Jong 2015). Backcross hybrids to *B. rapa* are aneuploid, they have the AA genome plus a variable (0–9) number of C chromosomes. Despite considerable sampling effort, backcross plants have not been found in the field in the UK or the Netherlands. Using AFLP-markers Luijten et al. (2015) found no evidence of introgression of crop genes from *B. napus* into wild *B. rapa* populations, suggesting that backcrosses are not fit. Despite their aneuploidy, backcross plants grew only slightly less than their parents in a growth room (de Jong, Escobedo Quevedo, van der Veen-van Wijk, & Moshgani 2017) and in the field (Hauser, Jørgensen, & Ostergard 1998; Rose et al. 2009). This raises the question whether backcross hybrids are less fit to survive due to other factors? In the field slugs greatly preferred *B. napus* over *B. rapa* seedlings and excluding slugs from plots with germinating seeds resulted in 4.3–26.5 times higher recruitment rates for different *B.*

napus varieties and 1.9 times higher recruitment for wild *B. rapa* (Moshgani, Kolvoort, & de Jong 2014). Slug herbivory is therefore potentially a relevant factor to consider for BC₁ hybrids.

To compare the amount of slug herbivory on parents and BC₁ hybrids we performed three choice experiments. First we examined herbivory by the slug *Arion lusitanicus* on leaves of one *B. rapa* accession (collected near Maarsse, the Netherlands), one *B. napus* variety and its corresponding BC₁ hybrid. In three sub experiments we used widely different *B. napus* varieties, each with their corresponding BC₁ hybrid and kept the same *B. rapa* accession for comparison. If defence traits were heritable and additive we expect that the rank order for herbivory in the BC₁ matches that in the corresponding *B. napus* parents (the maternal parent *B. rapa* was the same in all our crosses). The aneuploid BC₁ plants were expected to be variable, due to the different numbers of C-chromosomes they contain. In choice experiment 2 we compared the three BC₁'s. In choice experiment 3 four different *B. napus* varieties were presented simultaneously to slugs. Finally we did a no-choice experiment in which a slug was presented with abundant food of only one source. Glucosinolates (GS) are known defence compounds against herbivores in the Brassicaceae (Hopkins, van Dam, & van Loon 2009; Moshgani et al. 2014). DNA amount of the BC₁ is highly correlated with the number of unpaired C-chromosomes that these plants contain (de Jong et al. 2017). Therefore both GS content and DNA amount were measured as explanatory factors for the amount of herbivory.

Materials and methods

The accession *B. rapa*, for which seeds were collected along a roadside in Maarsse (the Netherlands), was the maternal parent in all crosses we made. This accession was self-incompatible under the conditions in the growth room; without hand pollination or after application of self-pollen to stigmas no seeds were produced. Seeds from this accession had a median GS concentration of 72.08 $\mu\text{mol/g DW}$ (de Jong, Tudela Isanta, & Hesse 2013). Three *B. napus* cultivars were used as paternal parents; Hornet is a modern double-zero cultivar with a GS concentration in seeds of 16.23 $\mu\text{mol/g DW}$. The old cultivar Mansholt (Mansholt's Hamburger) dates from 1899 and is maintained by the Centre of Genetic Resources of Wageningen University. Cultivar Mansholt had GS concentrations in seeds of 54.82 $\mu\text{mol/g DW}$. We collected seeds from the accession Utrecht in the summer of 2009 at the surroundings of the Cereol seed-processing factory in Utrecht that closed in 2001. This accession therefore has some ability to form feral populations. Accession Utrecht had GS concentration in seeds of 57.88 $\mu\text{mol/g DW}$. The three chosen cultivars of *B. napus* were therefore quite different. We made F₁'s by taking pollen from *B. napus* and placing this on stigmas of *B. rapa* flowers. To check our method we measured DNA value of the F₁ seeds formed and the DNA

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