Seed Science Research (2016) **26**, 245–253
doi:10.1017/S0960258516000118
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Dynamics of dormancy during seed development of oilseed rape (*Brassica napus* L.)

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(Received 21 January 2016; accepted after revision 14 April 2016; first published online 19 May 2016)

Abstract

Seed dormancy is a critical factor in determining seed persistence in the soil and can create oilseed rape (*Brassica napus* L.) volunteer problems in subsequent years. A 3-year field trial in south-west Germany investigated the effects of seed maturity on primary dormancy and disposition to secondary dormancy of ten oilseed rape varieties (lines) in 2009 and 2010, and of five imidazolinone-tolerant varieties (hybrids) in 2014. Fresh seeds were sampled weekly from about 30 d after flowering (DAF) until full maturity and tested for dormancy on the day of seed collection. Primary dormancy decreased from a high level of 70–99% at 30–40 DAF to 0–15% after 7–14 d, coinciding with embryo growth and depending on variety and year. For some oilseed rape varieties, 30–50% primary dormancy was still present in mature seeds. Depending on variety, disposition to secondary dormancy was nearly zero at the early stage of seed development, increased to its highest level during development, and decreased afterwards. Some varieties maintained a high level of secondary dormancy at maturity or during the entire seed development period. The correlation between primary dormancy and secondary dormancy was significantly positive at early seed development ($r = 0.95$, 50 DAF), but declined in mature seeds. Environmental conditions during ripening are also expected to affect dormancy dynamics. The deeper insights into dormancy formation of oilseed rape provide the possibility to improve harvest time and harvest method, and to better assess the potential for volunteer oilseed rape in following crops.

Keywords: abscisic acid, canola, dormancy, harvest date, seed bank, volunteers

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Introduction

Volunteer oilseed rape (*Brassica napus* L.) is an issue of concern due to the difficulty of chemical control of volunteers in a sown crop, especially when the varieties of oilseed rape are tolerant to specific herbicides such as imidazolinone. The emergence of volunteer oilseed rape is strongly dependent on seed persistence in the soil seed bank, which can last up to 11 years (Lutman *et al*., 2003). Secondary dormancy, induced by external environmental conditions such as dryness, darkness or oxygen deficiency (Pekrun *et al*., 1997, 1998) is a crucial contributor to seed persistence (Pekrun *et al*., 1998; Gulden *et al*., 2003, 2004a), in interaction with varieties (Gruber and Claupein, 2007a; Messéan *et al*., 2007; Weber *et al*., 2014). Gruber *et al*. (2010) found that 60% of initially buried seeds of a high-dormancy variety were still viable after 4.5 years of burial in the soil, while only 8% of a low-dormancy variety survived. Accordingly, a 30-fold increase in volunteer oilseed rape was recorded after growing and harvesting a high-dormancy variety compared to a low-dormancy variety in spring of the first following crop of winter wheat (Weber *et al*., 2014).

In contrast to secondary dormancy, primary dormancy is expressed in underdeveloped embryos and is controlled by phytohormones (mainly abscisic acid, ABA) (Hilhorst, 1995; Baskin and Baskin, 2004), preventing pre-harvest sprouting on the mother plant. Primary dormancy has previously been shown to be low (Momoh *et al*., 2002; Gruber *et al*., 2004; Gulden *et al*., 2004a) or nearly absent in fully mature seeds of oilseed rape (Schlink, 1993). Evidence has been found that primary dormancy may sometimes be present at harvest but that it decreases with the duration of dry storage (Gruber *et al*., 2004; Haile and Shirtliffe, 2014).

Dormancy dynamics are probably linked to a set of environmental conditions (e.g. precipitation or temperature) during the crop growth period. There appears to be a link between secondary dormancy and year (Gruber *et al*., 2009). For example, environmental conditions generally considered 'optimal' for seed yield have been shown to result in comparatively high levels of dormancy in winter oilseed rape

https://doi.org/10.1017/S0960258516000118 Published online by Cambridge University Press

(Schatzki *et al.*, 2013a), and Gulden *et al.* (2004a) showed that the environment contributed 0.1–4.5% to secondary dormancy in spring oilseed rape.

Neither the degree of primary dormancy of oilseed rape nor how long it is able to express secondary dormancy before harvest is well understood. This information could be especially relevant for oilseed rape fields that have been damaged by hailstorms in the weeks before harvest, to assess the potential of their seeds both to fall dormant and to result in volunteers in following crops. In two studied oilseed rape varieties, primary dormancy decreased over time during seed development, while secondary dormancy tended to increase (Haile and Shirtliffe, 2014). In fully mature oilseed rape seeds, there is a weak positive correlation between primary dormancy and secondary dormancy (Schatzki *et al.*, 2013b) but this has not been observed with respect to different stages of seed development. Whether there is an interaction between primary and secondary dormancy in oilseed rape and, if there is, how this interaction occurs during seed development are important for understanding seed dormancy in oilseed rape. If a correlation between them could be demonstrated, prediction of secondary dormancy by the level of primary dormancy would be possible. The objectives of this study were to determine the development of primary dormancy and secondary dormancy in oilseed rape, and, further, to find correlations between these during seed development.

Materials and methods

Field trials

Field trials were conducted in the years 2009, 2010 and 2014 at the experimental station Ihinger Hof (IHO) of the University of Hohenheim, south-west Germany (48°45′N, 8°56′E) on a loam soil. Mean annual temperature is 7.9°C and mean precipitation is 690 mm. Mean daily temperatures from flowering to harvest of oilseed rape (May–July) in 2009, 2010 and 2014 were 16.1, 15.8 and 15.7°C, respectively. Cumulative precipitation during this period in the 3 years was 362, 275 and 255 mm. Weather details are provided in supplementary Fig. S1. Daily temperature was calculated based on the mean hourly air temperature at 2 m above soil, and cumulative precipitation was derived from the daily rainfall. Weather data were obtained from the experimental station Ihinger Hof.

The trials were arranged in a randomized block design with four parallel blocks including ten line varieties of winter oilseed rape in 2009 and 2010 and five hybrid imidazolinone-tolerant (IT) oilseed rape varieties in 2014 per block. There were four field replicates per variety with a plot size of 4 m × 8 m in all 3 years. Seeds were sown on 27 August 2008, 29 August 2009 and 21 August 2013, with a sowing density of 50 seeds m^{-2}. Pest control and fertilization were performed according to the best management practice at that location.

Flowers in full bloom of the main inflorescence of 50 randomly chosen individual plants per variety and replicate were marked in 2009 and 2010, and 30 plants per variety and replicate in 2014, in the first week of May. The label was placed within the inflorescence, below the cohort of recently opened blossoms, to indicate the flowering time of these individual flowers. About 1 month after flowering, the first five pods of the main inflorescences directly above the label of five marked plants per harvest date were picked by hand at weekly intervals in all years (supplementary Table S1). In 2009 (eight harvest timings) and 2010 (nine harvest timings), five varieties (Smart, Express, Compakt, Splendor and Nemax) were harvested first, and the remaining five varieties (Lilian, Charly, Beauty, Ladoga and Komando) were harvested 2 d later, due to different flowering stages between two variety groups; ten varieties were harvested at the final timing in 2010. In 2014 (six harvest timings), all five varieties were harvested on the same day at each harvest.

Assessment of primary and secondary dormancy

The seeds of the five pods were removed from the siliques, pooled and then tested for primary dormancy and secondary dormancy according to the Hohenheim Standard Dormancy Test (Weber *et al.*, 2010) on the same day of seed collection. The test of secondary dormancy is comprised of three sequential processes. First, dormancy induction: 100 seeds per variety and harvest date in four laboratory replicates were imbibed in 8 ml of a polyethylene glycol 6000 solution (354.4 g l^{-1}, −15 bar; Michel and Kaufmann, 1973) in 9-cm plastic Petri dishes with double layers of filter paper. The Petri dishes were then put in metal boxes lined with black film to exclude any light and water evaporation, and were transferred to an incubator (20°C) for 14 d. Second, germination of non-dormant seeds: seeds were transferred to new Petri dishes equipped with double layers of filter paper and 6 ml deionized water in darkness at 20°C (14 d). During this period, seeds that were not induced into dormancy germinated and were removed from Petri dishes under a green safety light (500–600 nm). Third, dormancy breaking: non-germinated seeds were subjected to alternating light and temperature (12 h, 3°C, darkness/12 h, 30°C, light) for 7 d; germinated seeds in this process were considered to be induced into secondary dormancy in the first process. Seeds that germinated in the above three processes were considered viable. Intact seeds that did not germinate after dormancy breaking were

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considered dead or unable to germinate due to any other reasons; usually none or very few of these seeds existed. Secondary dormancy level was the proportion of induced dormant seeds over the total number of viable seeds used in the assays.

A parallel test for primary dormancy included the same two latter processes, germination of non-dormant seeds in darkness and dormancy breaking, but excluded a preceding dormancy induction in polyethylene glycol solution. Seeds that did not germinate before dormancy breaking were declared primarily dormant. Primary dormancy level was the proportion of dormant seeds over the total number of all viable seeds found in a sample. Seed viability was the proportion of the sum of any germinated seeds in a sample (during germination test and dormancy breaking) to all seeds used in the sample (Gruber *et al*., 2004; Weber *et al*., 2010).

Secondary dormancy in the fourth to ninth harvests in 2010 and in all harvests in 2014 was tested; primary dormancy was tested for seeds harvested at each harvest in all 3 years. Before starting the tests, broken or obviously mouldy seeds were excluded from seed lots.

Seed water content

Seed water content, as a measure of the developmental stage and grade of maturity of the seeds, was determined as follows: a portion of the harvested seed lot was dried in a 60°C oven for 48 h and seed water content was calculated as the per cent water content in the fresh seed weight. Additionally, embryos were removed from the seeds from another part of the harvested seed lot and photographed to document the stage of seed development.

Statistical analysis

Dormancy values were arc-sin transformed to stabilize variance and adjust the data to a standard normal distribution, with the following formula (Chatterjee and Hadi, 2012):

$$y = \arcsin\left(\sqrt{\frac{d + 3/8}{v + 3/4}}\right);$$

where y is the transformed value, d the number of dormant seeds, and v the number of viable seeds per replicate. The adjusted data were back-transformed for presentation. Analyses of variance for primary and secondary dormancy were performed according to the experimental design using the PROC MIXED procedure of the statistical software SAS 9.3 (SAS Institute, Cary, North Carolina, USA). All main effects for varieties, harvest date and their interactions were taken as fixed, while effects for laboratory replicates were taken as random. The correlations between primary dormancy and secondary dormancy at different harvests were analysed with the procedure PROC CORR of SAS 9.3.

Results

The water content of oilseed rape seeds harvested at different dates decreased continuously from approximately 80% at 28 d after flowering (DAF) to 9% when seeds were fully mature in 2009 and 2010 (Fig. 1). The decrease in seed water content ranged from 40% to 4% during the monitoring period of 2014. In 2009 and 2010, seed viability increased rapidly from nearly zero (28 DAF) to 100% (49 DAF) within 3 weeks, depending on variety, and remained at 100% until final harvest (Fig. 2). In 2014, seed viability was

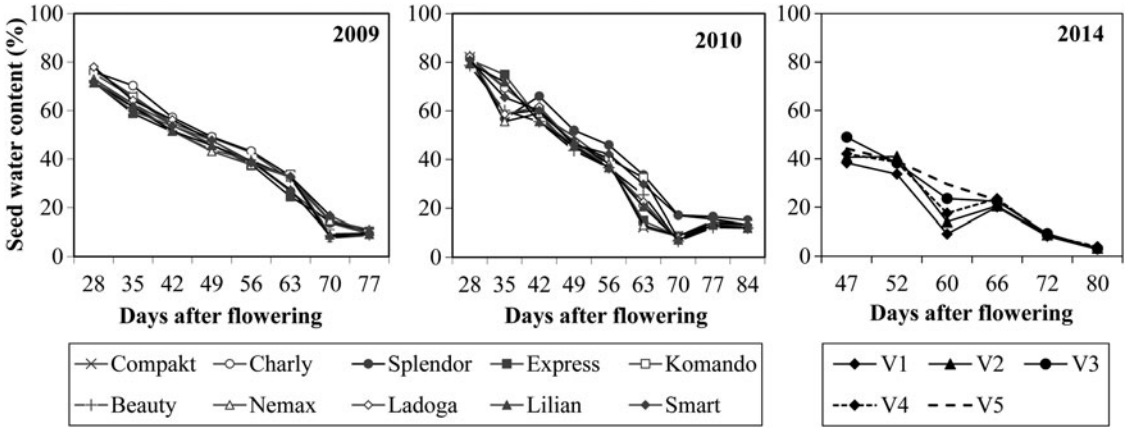


Figure 1. Seed water content (%) during seed development of ten oilseed rape varieties (lines) in 2009 and 2010, and of five hybrid imidazolinone-tolerant oilseed rape varieties (V1–V5) in 2014; for harvest dates see supplementary Table S1.

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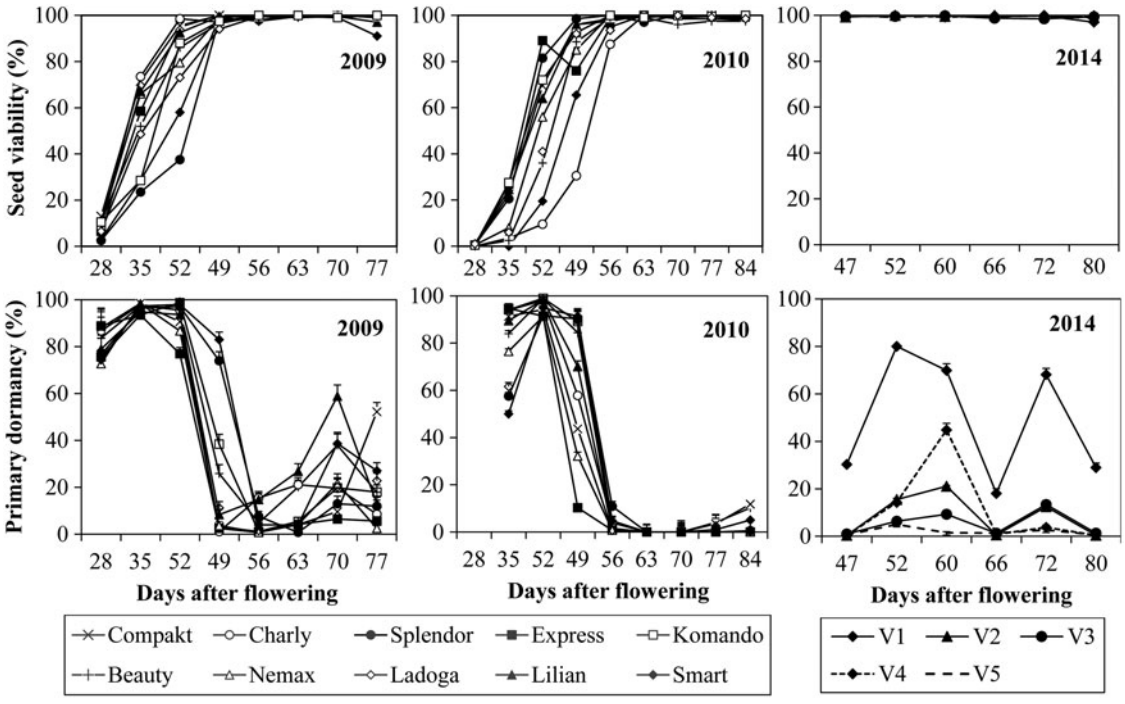


Figure 2. Seed viability (%) and primary seed dormancy (%) during seed development of ten oilseed rape varieties (lines) in 2009 and 2010, and of five hybrid imidazolinone-tolerant oilseed rape varieties (V1−V5) in 2014; for harvest dates see supplementary Table S1; error bars indicate standard error of mean.

already 100% at the first harvest, and lasted until the final harvest. Embryo development was exemplarily documented by images taken of the variety Smart (supplementary Fig. S2); the embryo was green at the beginning of the study, and over time it lost chlorophyll and turned yellow.

Variety, harvest date and their interaction had significant effects on both primary dormancy and secondary dormancy of oilseed rape (Table 1). Primary dormancy at the first harvest (28 DAF) in 2010 was not shown because of low seed viability (0.4%; Fig. 2). The primary dormancy values in viable seeds of ten line varieties were 73−89% at 28 DAF in 2009 and 50−95% at 35 DAF in 2010, depending on variety, peaking at 100% at 42 DAF, and decreased to zero in another 7−14 d (Fig. 2). Primary dormancy in varieties Compakt, Smart and Ladoga was still at 20−50% at the last harvest (*c.* 80 DAF) in 2009, but decreased to below 20% in 2010, similar to the other varieties. When seeds were fully viable (47 DAF) in 2014, primary dormancy was nearly zero for varieties V2−V5, was 30% for V1, and increased to the highest level at 52 or 60 DAF,

Table 1. Analysis of variance for primary dormancy and secondary dormancy of oilseed rape in 2009, 2010 and 2014, as affected by variety (V), harvest date (D) and their interactions (V × D)

Effect	DF	2009[a]		DF	2010[b]		DF	2014[c]	
		F value	*P*		*F* value	*P*		*F* value	*P*
Primary dormancy									
Variety (V)	9	15.9	<0.0001	9	9.7	<0.0001	4	609.8	<0.0001
Date (D)	7	1493.6	<0.0001	7	2537.8	<0.0001	5	210.0	<0.0001
V × D	63	16.1	<0.0001	63	13.6	<0.0001	20	21.3	<0.0001
Secondary dormancy									
Variety (V)	–	–	–	9	90.0	<0.0001	4	521.7	<0.0001
Date (D)	–	–	–	5	300.0	<0.0001	5	79.3	<0.0001
V × D	–	–	–	45	15.4	<0.0001	20	9.9	<0.0001

[a]Ten line varieties of winter oilseed rape, eight harvest dates; not analysed: secondary dormancy in 2009.
[b]Ten line varieties of winter oilseed rape, nine harvest dates; not analysed: primary dormancy at the first harvest because of low seed viability, secondary dormancy from the first harvest to the third harvest.
[c]Five hybrid imidazolinone-tolerant oilseed rape varieties, six harvest dates.

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followed by a non-linear decrease with time. At the final harvest in 2014, primary dormancy of varieties V2–V5 were nearly zero, but variety V1 still had 29% primary dormancy.

Secondary dormancy was initially low at 50–60 DAF (2010), reached a peak at about 70 DAF, depending on variety, and gradually decreased over time (Fig. 3). However, there were still four varieties that showed quite high secondary dormancy (>40%) at the last harvest in 2010. Particularly, secondary dormancy in variety Smart continued to increase from 31% at 49 DAF to 62% at 84 DAF, the highest dormancy among ten varieties at the final harvest. The levels of secondary dormancy tended to remain stable or to decrease slightly in the varieties V1, V2, V3 and V4 in the 2014 trial; V5 showed a clear decrease in secondary dormancy during that time.

As seed development progressed, the percentage values of both primary and secondary dormancy did not closely correlate with seed water content (data not shown), or with morphological seed development in general.

A significant correlation between primary dormancy and secondary dormancy was only found in the early stage of seed development (Table 2); correlation coefficients decreased from 0.58 at about 50 DAF to 0.09 at the final harvest in 2010, and deceased from 0.95 at 47 DAF to 0.69 at the final harvest in 2014. Both primary dormancy and secondary dormancy were not significantly correlated with cumulative precipitation and temperature during the harvest intervals (data not shown).

Discussion

This study indicates that primary dormancy decreased and the disposition to secondary dormancy (induced

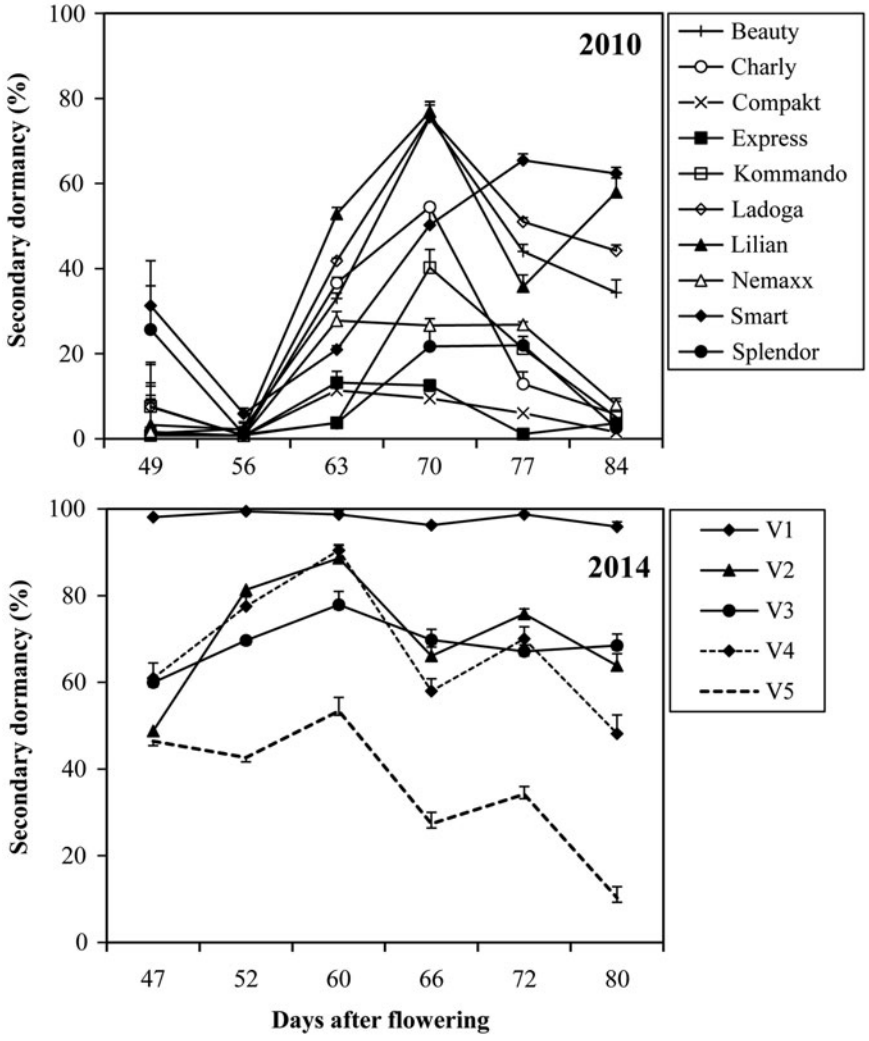


Figure 3. Dynamics of secondary dormancy (%) during seed development of ten oilseed rape varieties (lines) in 2010, and of five hybrid imidazolinone-tolerant oilseed rape varieties (V1–V5) in 2014; for harvest dates see supplementary Table S1; error bars indicate standard error of mean.

https://doi.org/10.1017/S0960258516000118 Published online by Cambridge University Press

Table 2. Correlation coefficients (*r*) between primary dormancy and secondary dormancy at different harvest dates during seed development of oilseed rape in the years 2010 ($n = 10$) and 2014 ($n = 5$); experimental station Ihinger Hof, south-west Germany; ten line varieties of winter oilseed rape in 2010 and five hybrid imidazolinone-tolerant oilseed rape varieties in 2014. DAF, days after flowering. For harvest dates see supplementary Table S1

Year	Correlation coefficient (*r*)					
2010	49 DAF	56 DAF	63 DAF	70 DAF	77 DAF	84 DAF
($n = 10$)	0.58*	0.18 ns	0.00 ns	0.00 ns	0.26 ns	0.09 ns
2014	47 DAF	52 DAF	60 DAF	66 DAF	72 DAF	80 DAF
($n = 5$)	0.95*	0.77	0.80 ns	0.73 ns	0.78 ns	0.69 ns

*$P < 0.05$; ns, not significant.

dormancy) of oilseed rape increased during the two months before typical harvest (normally at the end of July at the experimental site), in agreement with the findings of Gulden *et al*. (2004a), Gruber and Claupein (2007b), and Haile and Shirtliffe (2014). However, a rapid decline in primary dormancy in as short a period as 1 week, as seen in the present study (42−49 DAF in 2009, and 49−56 DAF 2010; Fig. 2) – coinciding with a rapid increase in seed viability and with embryo colour change from green (49 DAF) to yellow (56 DAF; supplementary Fig. S2) – had not been demonstrated to date. This rapid reduction in primary dormancy was not observed in 2014, probably due to the observed high seed viability of about 100% at first harvest (47 DAF). The rapid increase of seed viability at early seed development is supposed to depend on a critical growing period of embryos, after which almost all the seeds have a capacity to germinate if primary dormancy can be broken (Holdsworth *et al*., 1999, 2001). Based on the calculation of seed dormancy in the present study, all the dormant seeds were viable. Therefore, the observed high primary dormancy before the rapid decline at early seed development may be attributable to development of the embryos (Bewley, 1997; Haile and Shirtliffe, 2014). This process is assumed to depend on variety: primary dormancy in six out of ten varieties decreased to below 10% at 49 DAF, and the other four varieties (Smart, Splendor, Komado and Beauty) needed another 7 d (56 DAF) to reach the same dormancy level (in 2009). Using the water content of the seeds as an indicator of seed development, there was no apparent difference in water decrease between the varieties, so this would not explain differences in dormancy. Thus, the levels and changes in dormancy do not seem to be linked directly to morphological and physiological ripening alone. However, there seems to be a critical stage of development at which primary dormancy starts to decline. This stage may depend somehow on embryo development.

Various studies have documented the regulation of onset and maintenance of primary dormancy in many crop species by ABA (Finkelstein *et al*., 1985; Bewley, 1997; Gubler *et al*., 2005; Nambara *et al*., 2010). ABA content accumulated during seed development in oilseed rape, and reached its highest level at 35–40 DAF (Finkelstein *et al*., 1985), coinciding with the second to third harvests in 2009 and 2010 in our study, then declined with seed development. The appearance of ABA peaks during seed development can be influenced by environmental conditions, such as rainfall, temperature and humidity, surrounding mother plants (King, 1993; Romagosa *et al*., 2001; Chono *et al*., 2006). This may explain observed differences in the onset of the decline of primary dormancy in seed development between years.

Dormancy variation, particularly for primary dormancy, between varieties in the late seed development might be attributed to the temporal effects of environmental conditions (e.g. precipitation). However, correlations of primary and secondary dormancy with cumulative temperature and precipitation the week before harvest were not significant (not shown). Harvest timing experiments conducted at different locations or under controlled conditions could probably offer more robust data for detecting this relationship.

Secondary dormancy of most varieties used in the current study increased after the immature seeds achieved full viability, consistent with the findings of Haile and Shirtliffe (2014), then decreased to different degrees (Fig. 3). In oilseed rape, there is consensus that secondary dormancy decreases with storage time post-harvest (Gulden *et al*., 2004a), which is likely to be connected with the decline of secondary dormancy when seeds are still on the mother plants. With this in mind, this dormancy decline might be a continuous process in time, which starts before seed maturity and continues during seed storage. Also, the potential dynamics of secondary dormancy are dependent on the variety, as shown in Table 1 and Fig. 3. The importance of variety has been reported previously in European, Canadian and Chinese oilseed rape (Momoh *et al*., 2002; Gruber *et al*., 2004, 2009; Gulden *et al*., 2004a; Schatzki *et al*., 2013a, b), but these studies focused mainly on the mature seeds. The present study indicates that genotypic differences in secondary dormancy are initially small, but become greater with seed development. This result may provide some

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clues to understanding the formation and maintenance of secondary dormancy, if differences in genetic background between varieties can be detected clearly enough.

Similar to primary dormancy, secondary dormancy in oilseed rape is also presumed to be associated with ABA (Gulden *et al*., 2004b; Fei *et al*., 2007, 2009). More ABA-inducible genes were up-regulated in mature seeds of a high-dormancy oilseed rape variety compared to a low-dormancy variety when treated with polyethylene glycol; twice as much ABA was detected in freshly harvested seeds of a high-dormancy variety (Fei *et al*., 2007, 2009) and high-dormancy oilseed rape varieties seem to be more sensitive to ABA than low-dormancy varieties (Gulden *et al*., 2004b). Despite the complex mechanisms involved in the dynamics of secondary dormancy, which are not yet completely understood, the results of this study indicate that harvest before full seed maturity might lead to high dormancy levels (mainly secondary dormancy) in the seeds, but accompanied by low harvest losses (Price *et al*., 1996). Also, there seems to be a certain degree of primary dormancy in mature seeds, which could lead to a soil seed bank even if there are no further dormancy-inducing conditions. In contrast, late harvest can result in low-dormancy seeds, but the harvest losses will be great (e.g. *c*. 5000 seeds m^{-2}; Lutman *et al*., 2005). With the improvement of harvesting techniques and breeding (pod-shattering resistance), the latter option could become a more acceptable way to reduce volunteer problems in a crop rotation with oilseed rape. However, a problem would arise if, for example, hailstorms cracked unripe pods and fresh seeds dropped (e.g. more than 280 hailstorms were recorded in June and July 2014 across Germany; ESWD, 2014). These fresh seeds with high levels of primary dormancy could lead to seed survival in the soil without further inductive environmental conditions, and could be induced into secondary dormancy by environmental conditions such as dryness (Pekrun *et al*., 1997, 1998). Based on our results, seed dormancy (primary and secondary dormancy) is variety-dependent during late seed development; i.e. varieties with low dormancy represent a lower risk of a soil seed bank after hailstorms or after early harvest.

A significant correlation between primary dormancy and secondary dormancy at early stages of seed development in oilseed rape, as shown in the current study, could be used to predict roughly the level of secondary dormancy from a specific stage of development. Because of environmental effects, however, this prediction would be most useful for plants grown under controlled conditions, such as in a greenhouse. In a different plant, *Arabidopsis thaliana*, it was shown that the state of primary seed dormancy can affect secondary dormancy induction after harvest (Auge *et al*., 2015). In this case, secondary dormancy was more easily induced in seeds with higher primary dormancy than in seeds with low or no primary dormancy of the same *A. thaliana* variety that matured under a different maternal environment. This may also occur in oilseed rape during late seed development, based on the positive correlation between primary dormancy and secondary dormancy, but depends on the year and the variety.

Because both primary and secondary dormancy are present in immature seeds of oilseed rape, both timing and techniques of harvest should be reconsidered. Early harvest, for example windrowing before full maturity, may reduce harvest losses caused by pod shattering, but could lead to higher seed dormancy. Afterripening, which was not tested in this study, would further decrease dormancy. However, in the context of increasingly worldwide use of the combine harvester, harvest at full maturity or late harvest is preferred but could cause large harvest losses. Under this harvest scenario, selection of low-dormant oilseed rape varieties would be a simple and feasible strategy to reduce the risk of soil seed bank and volunteers in a crop rotation.

Supplementary material

To view supplementary material for this article, please visit http://dx.doi.org/10.1017/S0960258516000118

Acknowledgements

The authors would like to thank Andrea Rückle for excellent technical support, the staff of the experimental station Ihinger Hof for excellent field management, Dr Sebastian Munz, Jialu Xu and Kathleen Regan for their useful comments, and the China Scholarship Council (CSC) for their support.

Financial support

Financial support was provided by the German Federal Ministry of Education and Research (BMBF 0315211A) and China Scholarship Council (CSC 201206350064).

Conflicts of interest

None.

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https://doi.org/10.1017/S0960258516000118 Published online by Cambridge University Press

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