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Seed dormancy in F_1 and F_2 generations of imidazolinone-tolerant oilseed rape at different locations

Dormanz in Samen der F_1- und F_2- Generation von Imidazolinon-tolerantem Raps an unterschiedlichen Standorten

Abstract

The introduction of imidazolinone-tolerant oilseed rape (*Brassica napus*; Clearfield®, CL OSR) meets with skepticism on volunteer control. This study examined the disposition to secondary seed dormancy of 15 CL OSR genotypes at two locations in south-west Germany in 2012/2013 (trial 1) between sown seed (F_1) and harvested seed (F_2), and effects of maternal environment on dormancy disposition on CL and non-CL OSR in 12 locations in Germany in 2011/2012 (trial 2). The CL genotypes differed in dormancy from 0 to 95.7% in the F_1 generation and from 3.5 to 77.9% for their corresponding offspring (F_2). The dormancy levels of the F_1 generations corresponded to that of the F_2 generations. This correlation was higher if seeds derived from flowers which have been isolated in the plastic bags and thus outcrossing has been prevented. Seed lots from individual isolated F_1 plants deviated in dormancy by up to 30% from the mean of all isolated plants of a specific genotype. In trial 2, seeds from low dormancy genotypes tended to respond more strongly to maternal environment than high dormancy genotypes did. Precipitation during the period of ripening was positively correlated with dormancy (R = 0.78). Overall, breeders can use the dormancy values of the F_1 generation to assess the potential of dormancy in their offspring, which are those seeds that are relevant for causing volunteers if several other external conditions are fitting.

Key words: Clearfield, *Brassica napus*, volunteers, secondary dormancy, maternal environment, precipitation, hybrids

Zusammenfassung

Die Einführung von Imidazolinon-tolerantem Raps (*Brassica napus*; Clearfieldraps, CL Raps) wird speziell im Bereich der Kontrolle von Durchwuchsraps mit Skepsis aufgenommen. Die vorliegende Studie untersuchte die Neigung zu sekundärer Dormanz bei 15 CL Rapsgenotypen an zwei Standorten in Deutschland im Jahr 2012/2013 (Versuch 1) sowie Auswirkungen der maternalen Umgebung auf die Dormanzneigung der gebildeten Rapssamen in CL und nicht-CL Raps (insgesamt 8 Sorten) an 12 Standorten in Deutschland in den Jahren 2011/2012 (Versuch 2). Die CL-Genotypen variierten in der Dormanzneigung von 0 bis 95,7% in der F_1-Generation (Hybridsaatgut) und von 3,5 bis 77,9% in der entsprechenden F_2-Generation (Erntegut). Das Niveau der Dormanz in der F_2 entsprach dem in der F_1, sowohl bei isolierten als auch in etwas geringerem Maß bei nicht-isolierten Pflanzen. Bei allen geprüften Genotypen setzten sich die angebauten F_1-Pflanzen aus Einzelpflanzen mit zum Teil unterschiedlicher Dormanzneigung in der jeweiligen Nachkommenschaft zusammen; zum Teil wich die Dormanz der F_2 einer Einzelpflanze bis zu 30% vom Sortenmittel ab.

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Unterschiede in der Dormanz zeigten sich in zwei CL Raps-Genotypen und sechs nicht-CL-Genotypen an 12 Standorten (trial 2/Versuch 2). Samen von niedrig dormanten Genotypen reagierten tendenziell stärker auf die maternale Umgebung als Samen von hoch dormanten Genotypen. Niederschläge während der Reifezeit korrelierten positiv mit der Dormanz (R = 0,78). Insgesamt können Züchter die Dormanzwerte der F_1-Generation nutzen, um das Potential der Dormanz jener Samen in der F_2-Generation zu bewerten, die zu Durchwuchs führen könnten.

Stichwörter: Clearfield, *Brassica napus*, Durchwuchs, sekundäre Dormanz, maternale Umgebung, Niederschlag, Hybride

Introduction

The potential for gene dispersal of oilseed rape (*Brassica napus* L.; OSR) by seed, and thus by volunteers emerging from the soil seed bank, is an issue of discussion especially for herbicide tolerant OSR. Volunteer OSR is a result of high seed loss before and during harvest (LUTMAN et al., 2003, 2005), soil tillage operations after harvest, and the capacity of the seed to fall dormant (GULDEN et al., 2003; GRUBER et al., 2004a; WEBER et al., 2013). Volunteers can emerge in following crops within crop rotations grown in the same field for several years due to long-term seed persistence in the soil seed bank of up to 10 or more years (LUTMAN et al., 2005; MESSÉAN et al., 2007; D'HERTEFELDT et al., 2008). The forthcoming introduction of imidazolinone-tolerant oilseed rape (Clearfield®; CL OSR) revived the discussion about volunteers particularly because these volunteers are able to survive herbicide applications from the imidazolinone group, as well as related groups which inhibit acetolactate synthase (ALS). As chemical control of CL volunteers has to rely on a limited number of active ingredients and because chemical control of OSR volunteers in sown OSR is not possible, further agronomical strategies have to be developed and to be assessed to minimize volunteers.

Seed persistence of OSR is associated with the disposition of seeds to secondary dormancy. Soil seed banks of OSR from high dormant varieties were clearly larger than seed banks from low dormant varieties, as observed in Canada and Germany (GULDEN et al., 2003; WEBER et al., 2014). OSR presents no or very little primary (non-induced) dormancy at harvest (MOMOH et al., 2002; GRUBER et al., 2004b), and develops secondary dormancy (thereafter referred to as dormancy) under specific conditions such as osmotic stress and darkness (PEKRUN et al., 1998). The disposition to dormancy is heritable, and the heritability was calculated to be 96–97% (SCHATZKI et al., 2013a; WEBER et al., 2013). In a group of 16 Canadian commercial OSR (Canola) varieties, the contribution of genotype to dormancy ranged from 44% to 82% (GULDEN et al., 2004a). Five QTLs have been recently found which explain 42% of the total dormancy in OSR (SCHATZKI et al., 2013b). Hence, selection of or breeding for low dormant varieties seems to be an effective strategy to reduce or to avoid soil seed banks of OSR and to prevent volunteers in the crop rotation. Particularly the increased – perceived or real – incidence of volunteer OSR in sown OSR could be controlled that way.

The mechanism of seed dormancy formation and heritability is complex, based on different physiological pathways and is not yet fully understood in many weeds and crops (BASKIN and BASKIN, 2005; FEI et al., 2007, 2009; FINKELSTEIN et al., 2008). The expression of seed dormancy is related to the genotype (FOLEY and FENNIMORE, 1998) and to maternal environmental conditions. Also in OSR, environmental conditions during growth and maturation of the seeds seem to affect the disposition to dormancy expression (GULDEN et al., 2004a; GRUBER et al., 2009; SCHATZKI et al., 2013a). For instance, the influence of the pre-harvest environment during seed maturation on seed dormancy accounted for 0.1–4.5% of total dormancy variation (GULDEN et al., 2004a).

Many OSR genotypes including genotypes with altered traits or ingredients have been analysed for dormancy in the past (GULDEN et al., 2003; GRUBER et al., 2004b; WEBER et al., 2010). However, nearly all results from dormancy were derived from open-pollinated varieties, and the dormancy of hybrids, particularly of imidazolinone-tolerant varieties (Clearfield®, CL), are not yet widely tested or tested at all, although CL OSR is being planted widely in Canada and the USA (BRIMNER et al., 2005). Furthermore, the differences between open-pollinated and hybrid OSR genotypes were seldom included in previous studies, and a possible segregation of dormancy in the F_2 generation of hybrid OSR was not yet analysed. Additionally, the effects of maternal environment on formation of potential seed dormancy and dormancy stability within population of a given genotype were not explicitly studied.

Therefore, the aim of the study was (i) to investigate for the first time a number of hybrid CL OSR genotypes, some of them launched in the European market, for their disposition to secondary dormancy in F_1 and F_2 generations, and (ii) to investigate impacts of the maternal environment on disposition to secondary dormancy.

Results are derived from two experimental approaches in the field: trial 1 with 15 genotypes grown at two locations; trial 2 with eight genotypes at 12 locations. Both varieties and breeding lines were used in this research, but in order to improve readability both of them were defined as "genotypes".

Materials and methods

Trial 1

The trial was performed in 2012/2013 as a randomized complete block design (four replicates) with 11 CL hybrid genotypes (imidazolinone-tolerant, Clearfield®) at the experimental station Ihinger Hof (IHO) of the University of Hohenheim and 15 CL hybrid genotypes at the location Hohenheim (Table 1).

Table 1. Oilseed rape genotypes (hybrids) used in two field trials, provided by three breeding companies. CL, Clearfield oilseed rape; non-CL, non-Clearfield oilseed rape. Trial 1: two locations; Trial 2: 12 locations, not presented
Rapsgenotypen (Hybridraps, von drei Züchtern), angebaut in zwei Feldversuchen. CL, Clearfieldraps; non-CL, kein Clearfieldraps.- Versuch 1 auf zwei Standorten, Versuch 2 auf 12 nicht genannten Standorten

Genotype		Trial 1		Trial 2
No.		Hohenheim	IHO	
1	CL	x	x	–
2	CL	x	x	–
3	CL	x	x	–
4	CL	x	x	–
5	CL	x	x	–
6	CL	x	x	–
7	CL	x	x	–
8	CL	x	–	–
9	CL	x	x	x
10	CL	x	x	x
11	CL	x	–	–
12	CL	x	–	–
13	CL	x	x	–
14	CL	x	–	–
15	CL	x	x	–
16	Non-CL	–	–	x
17	Non-CL	–	–	x
18	Non-CL	–	–	x
19	Non-CL	–	–	x
20	Non-CL	–	–	x
21	Non-CL	–	–	x

Both experimental locations were located in southwest Germany on a loamy soil and differed in precipitation and temperature, with 820 mm and 9.0°C for IHO and 710 mm and 9.8°C for Hohenheim; precipitation and temperature in the growing season of winter OSR in 2012/2013 at both locations is provided in Fig. 1. The CL OSR genotypes were sown at a density of 50 seeds m^{-2} with a plot size of 4 × 5 m for Hohenheim and 3×8 m for IHO on 27th and 29th August 2012, respectively. Weeds, pests and diseases were controlled according to the best management practice.

The main inflorescences of 10 randomly chosen individual plants of each plot at Hohenheim were isolated shortly before the beginning of the flowering stage using perforated plastic bags, ensuring aeration but excluding

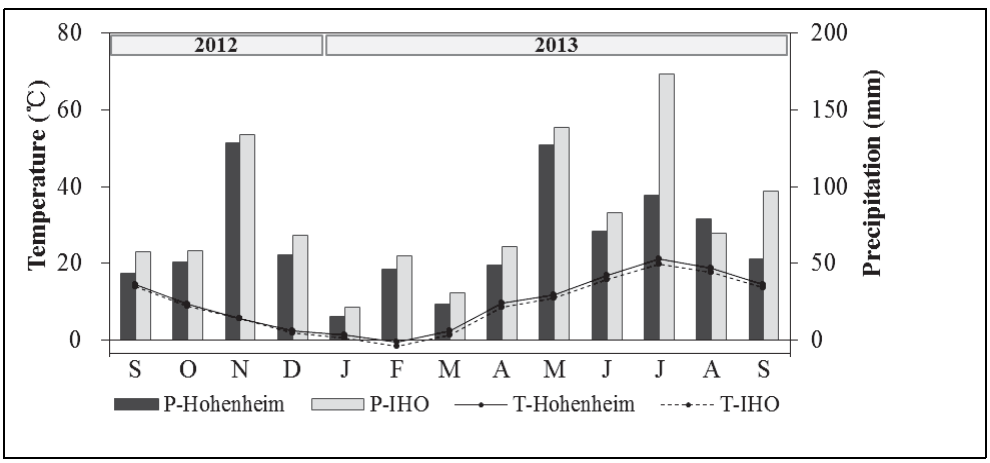

Fig. 1. Temperature (T, line) and precipitation (P, columns) in the growing season for winter oilseed rape in 2012/2013 at the locations of Hohenheim and Ihinger Hof (IHO).
Temperatur (T, Linie) und Niederschlag (P, Säulen) während der Anbauperiode von Winterraps 2012/2013 auf den Versuchsflächen Hohenheim und Ihinger Hof (IHO).

cross-pollination. The bags were lifted twice a week to provide enough space for the covered inflorescences to grow, and they were removed at early stage of pod formation. The beginning of flowering was noted on a label for each plant.

Hand harvest of the individual plants was done on 19th July 2013. The seeds from four out of the 10 isolated individual plants per plot with four replicates were harvested and kept separately (main stems from the individual plants; "IP") and the other six isolated plants were harvested and then mixed together by hand ("mixed-IP"). The remaining non-isolated plants in each plot were separately harvested by a plot combine harvester on 3rd August at IHO and 5thAugust 2013 at Hohenheim. After harvest, all the seed lots harvested by hand and by combine harvester were stored at room temperature, about 20°C, until the laboratory dormancy tests started.

The F_1 seeds of 15 CL genotypes were produced and harvested in 2011 by the seed companies. Genotypes 7–15 were treated with insecticides (thiamethoxam, active ingredient in Cruiser®) at delivery. All the seeds were stored under 10°C in an incubator until the dormancy test was conducted in February 2013. The F_2 seeds harvested in trial 1 were tested for dormancy and for viability during August and September 2013.

Hohenheim Standard Dormancy Test was used to test seed dormancy and viability (WEBER et al., 2010). The test comprises the induction of secondary dormancy on a polyethylene glycol solution (354.4 g in one l H_2O, −15 bar) in darkness (14 days), the identification of non-dormant seeds on water under darkness (seven days), and finally a viability test of potential dormant seeds under alternating light and temperature conditions (12 h darkness 3°C/12 h light 30°C, seven days). Finally, the test provides dormancy value as a percentage of the number of dormant seeds/viable seeds.

Trial 2

Two CL hybrid genotypes and six non-CL hybrid genotypes (Table 1) from one seed company were grown by the company itself at 12 locations in 2011/2012. Harvested seeds (F_2 generation) were analysed for dormancy by the Hohenheim Standard Dormancy Test in September 2012. The seeds were delivered to the authors for analysis and stored at room temperature until dormancy testing. Weather data in 2012 from the 12 stations nearest to the experiment locations was collected from http://www.dwd.de (DWD, Deutscher Wetterdienst, 2014).

Analysis

Arc-sin transformation was used to stabilize variance and adjust the data to a standard normal distribution using the following formula according to CHATTERJEE and HADI (2012),

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

where y, d and v are the transformed value, the absolute number of dormant seeds and the absolute number of viable seeds per replicate, respectively. All the adjusted data was back-transformed for presentation. The analysis of variance was performed by PROC MIXED of the statistical software SAS 9.3 (SAS Institute, Carey, NC, USA). In trial 1, all main effects for the three factors (genotype, location, and isolation of flowers) and their interactions were taken as fixed in the mixed model, while effects for replicate and the main plot were taken as random; in trial 2, effects of genotype, location and their interactions were taken as fixed, while only effects of lab replicates were taken as random because there were no field replicates at each location. Correlations coefficients were calculated in SAS by the procedure PROC CORR.

Results

Trial 1

The analysis of variance showed highly significant effects of genotype, location, plant isolation, and their interaction on seed dormancy (Table 2).

Dormancy varied between genotypes after artificial dormancy induction from 0.4 to 95.7% in the sown F_1 generation, from 4.1 to 86.9% in the F_2 offspring for mixed-IP (mixed individual, isolated plants) seeds at Hohenheim, and from 3.9 to 78.6% and from 9.3 to 76.6% for seeds from non-isolated plants at Hohenheim and IHO in the F_2 generations, respectively (Fig. 2). According to the variation of dormancy in the F_1 generation, genotypes could be classified into a low-dormant group (from genotype 1 to 9) with a mean value of 10.1% and high-dormant group (from genotype 10 to 15) with a mean value of 83.6%. F_1 and F_2 generations were strongly correlated concerning their seed dormancy potential with R = 0.96 and 0.91 for mixed-IP seeds and non-isolated seeds in the F_2 generation, respectively (Fig. 2).

The dormancy values of non-isolated seeds in the F_2 generation between the two locations Hohenheim and IHO were significantly correlated with R = 0.84 and 1.0 for low-dormant and high-dormant groups, respectively (Fig. 3). Seven out of eight genotypes (no data for genotype 8 at IHO) in the low-dormant group showed significant differences in seed dormancy between two locations (group a; Fig. 3), whereas no significant difference was detected in the high-dormant group (group b; Fig. 3).

The comparison between mixed-IP and non-isolated seeds at the same location brought significant differences for two out of nine low-dormant genotypes and for five out of six high-dormant genotypes (Fig. 4). The correlation between mixed-IP and non-isolated seeds at Hohenheim was significant with R = 0.97, although the dormancy value of non-isolated seeds was 6.9 percentage points lower than that of mixed-IP seeds.

The isolated individual (IP) plants varied in the mean dormancy of their offspring (Fig. 5). Plant-to-plant dormancy variation was 63.4–97.5%, 61.6–97.2%, 19.1–90.9%, 6.4–40.7%, 10.3–66.1% and 8.9–51.9% for genotype 15, 14, 10, 9, 8 and 3 with mean values of 88.8, 81.7, 62.6, 19.6, 35.9 and 31.3%, respectively.

Table 2. F-values for the effects of genotype, location, isolation, and their interaction on secondary dormancy of winter CL OSR genotypes in the F_2 generations (harvested seeds) in two trials; trial 1: 15 genotypes at two locations; trial 2: eight genotypes at 12 locations

F-Werte für die Effekte von Genotyp, Standort, Isolation des Blütenstandes (Selbstung) und deren Wechselwirkungen auf Samendormanz von CL Winterraps in der F_2 Generation (Erntegut) aus zwei Versuchen; Versuch 1: 15 Genotypen an zwei Standorten, Versuch 2: acht Genotypen an 12 Standorten

Field trial	Effect	DF	F-value	P
1	Genotype (G)	14	155.6	< 0.0001
	Location (L)	1	33.1	< 0.0001
	Isolation (I)	1	36.8	< 0.0001
	G×L	10	3.4	0.0003
	G×I	14	2.7	0.001
2	Genotype (G)	7	421.3	< 0.0001
	Location (L)	11	55.2	< 0.0001
	G×L	74	4.7	< 0.0001

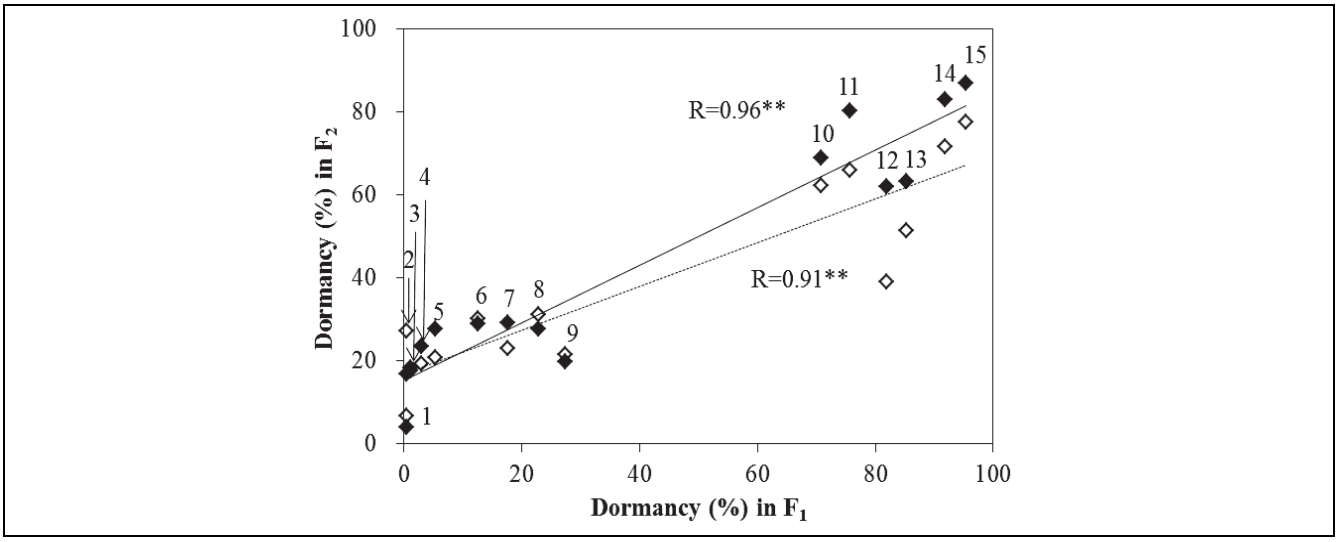

Fig. 2. Correlation of secondary dormancy (% dormant seeds/viable seeds after dormancy induction in the laboratory) of Clearfield oilseed rape between original hybrid seeds in F_1 and mixed isolated (♦ full line) and non-isolated seeds (◊ dashed line) in the F_2 generation. Isolated seeds of 15 genotypes in F_2 generation are derived from Hohenheim; dormancy values of non-isolated seeds of genotype 1–7, 9, 10, 13, 15 in F_2 generation are mean values across two locations, IHO and Hohenheim; genotype 8, 11, 12 and 14 in F_2 generation are from one location, Hohenheim. ** $P < 0.01$.

*Korrelation von sekundärer Dormanz (% dormante Samen/lebensfähiger Samen nach Dormanzinduktion im Labor) in Samen von Clearfieldrapssorten in Hybridsaatgut (F_1-Generation) und dem entsprechenden Erntegut (F_2-Generation; Mischung geselbsteter bzw. isolierter Einzelpflanzen je Sorte); ♦ durchgezogene Linie: Genotypen mit vergleichsweise niedriger Dormanzneigung; ◊ gepunktete Linie: Genotypen mit vergleichsweise hoher Dormanzneigung. Werte der F_2 für die frei abgeblühte Pflanzen der Genotypen 1–7, 9, 10, 13, 15 sind Mittelwerte aus den Standorten IHO und Hohenheim, Werte für die Genotypen 8, 11, 12, 14 nur vom Standort Hohenheim. ** $P < 0{,}01$.*

Field trial 2

Seed lots from two CL OSR and six non-CL OSR genotypes (Table 1) derived from 12 locations in Germany varied in dormancy depending on the location and on the genotype. The deviation in dormancy of a single genotype at a specific location from the mean of this genotype across all locations (location effects), was plotted against the deviation in dormancy of a single genotype at a specific location from the mean of this location across all genotypes (genotype effects; Fig. 6). The order of dormancy, from low to high, of these eight genotypes was genotype 17, 9, 16, 19, 10, 21, 18, and 20, and their mean dormancy levels across all locations were 42.1, 48.1, 67.7, 82.2, 84.3, 86.0, 87.9, and 90.0%, respectively (data not shown).

The closer a value is to the y-axis, the lesser the deviation of a genotype at this specific location is from the geno-

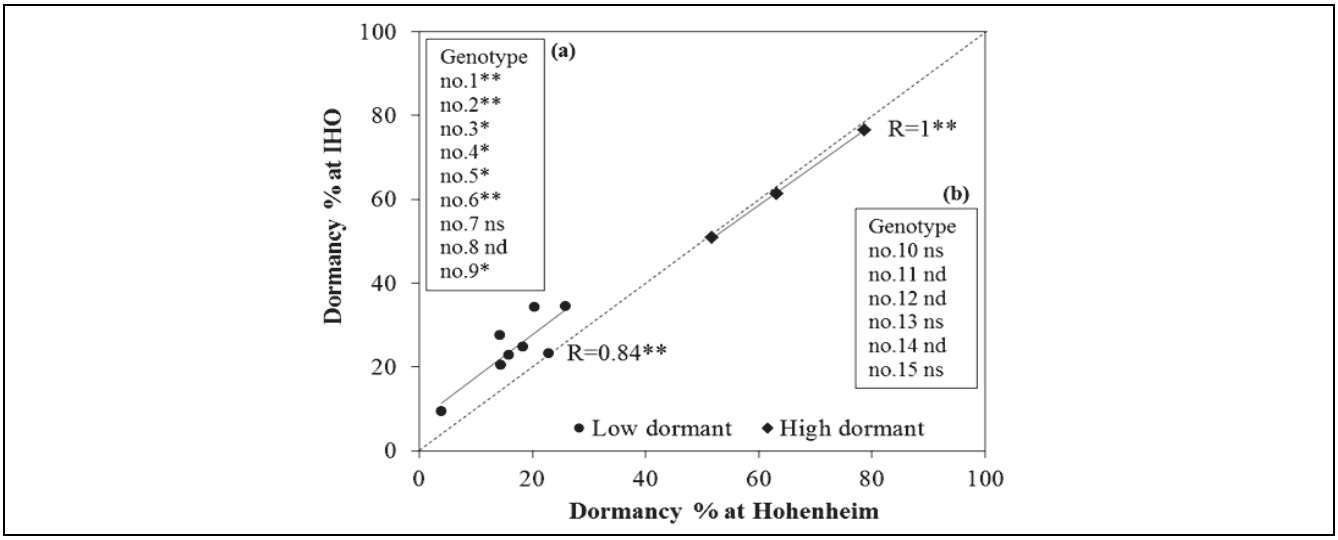

Fig. 3. Correlation of secondary dormancy (% dormant seed/viable seed after dormancy induction in the laboratory) in Clearfield oilseed rape seeds (• comparatively low dormant, ♦ comparatively high dormant) in the F_2 generation, harvested at the locations Hohenheim and IHO in 2013; the small frames (a, low dormant genotypes; b, high dormant genotypes) show the difference in dormancy between two locations of a given genotype. * $P < 0.05$; ** $P < 0.01$, ns not signifikant. Comparison within the same genotype at two locations; nd: no data available; dotted line represents the bisecting line of the graph.

*Korrelation von sekundärer Dormanz (% dormante Samen/lebensfähige Samen nach Dormanzinduktion im Labor) im Erntegut (F_2-Generation) von Clearfieldraps (• vergleichsweise niedrig dormante Genotypen, ♦ vergleichsweise hoch dormante Genotypen), geerntet auf den Standorten Hohenheim und Ihinger Hof im Jahr 2013. Die Kästchen (a, vergleichsweise niedrig dormante Genoytpen; b; vergleichsweise hoch dormante Genotypen) zeigen den Standortunterschied für die Dormanz des Erntegut jeweils eines Genotyps. * P < 0,05, ** P < 0,01, ns nicht signifikant; nd keine Daten verfügbar. Vergleich nur zwischen den Standorten innerhalb eines Genotyps.*

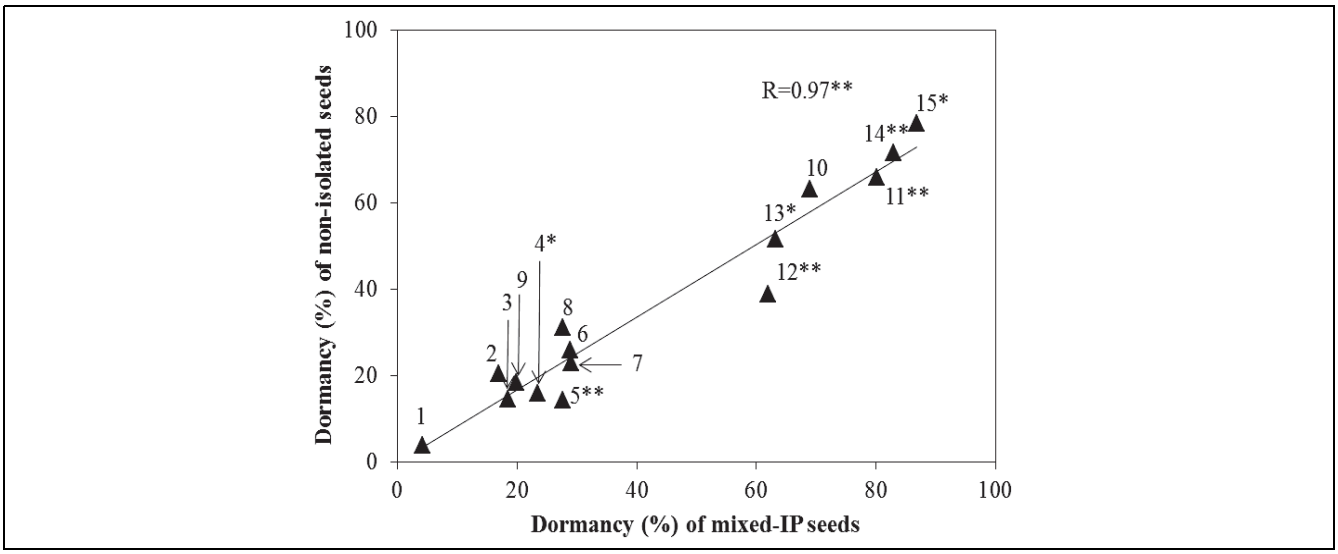

Fig. 4. Correlation of secondary dormancy (% dormant seeds/viable seeds after dormancy induction in the laboratory) in mixed-IP seeds and non-isolated seeds (both F_2 generation) of Clearfield oilseed rape, grown at the location Hohenheim. Mixed-IP: mixed seeds of isolated individual plants, non-isolated seeds: seeds from non-isolated plants. 1, 2 ... 15 are genotype numbers; * $P < 0.05$, ** $P < 0.01$, and ns not significant at $P < 0.05$; comparison within the same genotype between isolated seeds and mix-IP seeds.

*Korrelation von sekundärer Dormanz (% dormante Samen/lebensfähige Samen nach Dormanzinduktion im Labor) in Samen von Clearfieldraps aus dem gemischten Erntegut geselbsteter bzw. isolierter Einzelpflanzen („mixed-IP") und aus dem Erntegut offen abgeblühter Pflanzen („non-isolated seeds"; beides F_2-Generation) vom selben Standort (Hohenheim). * P < 0,05, ** P < 0,01, ns nicht signifikant bei P < 0,05.*

type mean across all locations. Regarding the locations, the closer a value is to the x-axis, the lesser the deviation of the location is from the location mean across genotypes. Locations with dormancy values close to the y-axis had led to less varietal variation. Genotypes with dormancy close to the y-axis responded comparatively little to location effects. Genotypes with lower dormancy (values below the x-axis) tended to respond more to effects

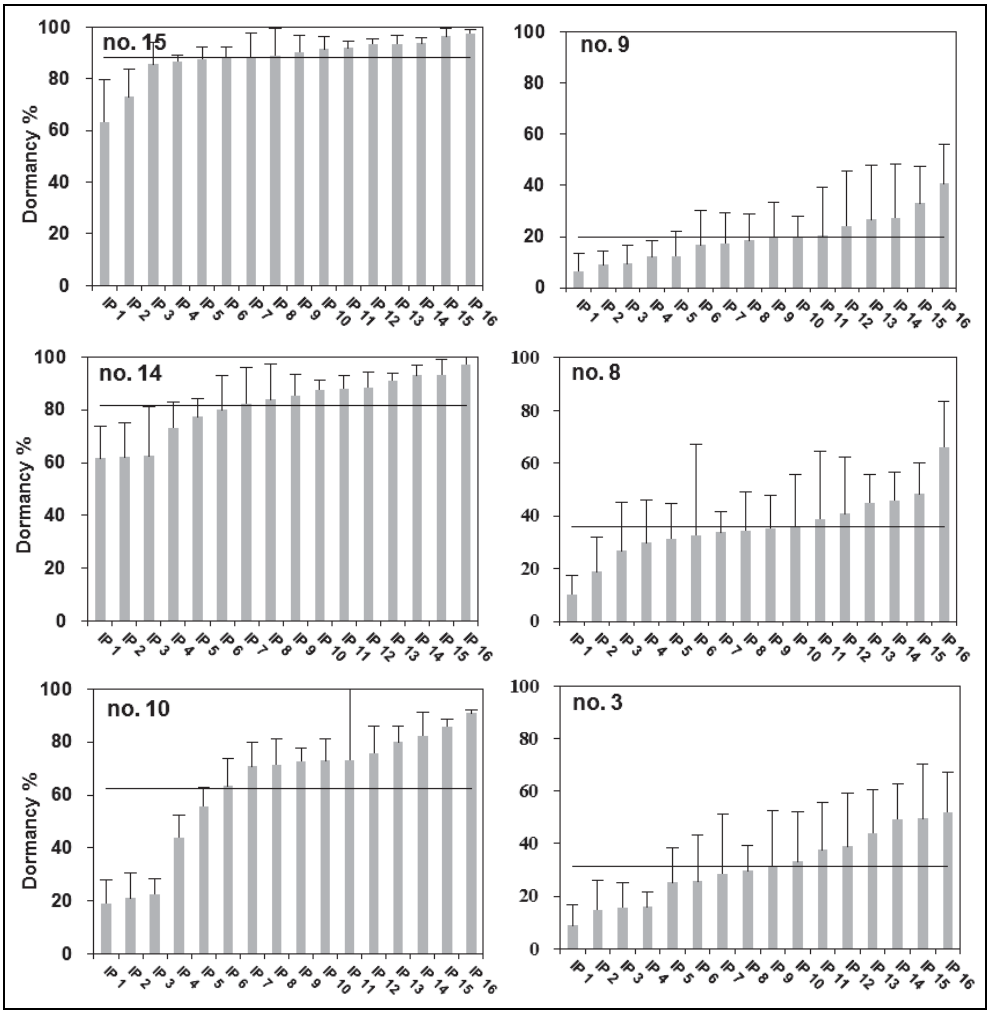

Fig. 5. Secondary seed dormancy (% dormant seed/viable seed after dormancy induction in the laboratory) in seeds harvested from 16 isolated individual plants (IP, four replicates of four individual plants) of six Clearfield oilseed rape genotypes (F_2 generation, harvest 2013, location Hohenheim). Horizontal lines stand for mean values of secondary dormancy (across individual IP-dormancy levels). Error bars = standard error of mean.
Sekundäre Dormanz (% dormante Samen/lebensfähige Samen) im Erntegut von 16 geselbsteten bzw. isolierten Einzelpflanzen (IP, vier Wiederholungen von vier einzelnen Pflanzen) von sechs verschiedenen Clearfieldraps-Genotypen (F_2-Generation, Ernte 2013, Standort Hohenheim). Horizontale Linien stehen für Mittelwerte der sekundären Dormanz aller geselbsteten Einzelpflanzen. Fehlerbalken = Standardfehler des Mittelwerts.

of the location than genotypes with higher dormancy. Location effects strongly correlated with genotype effects for genotype 9, 16 and 17, the dormancy levels of which were lower than the mean value of all genotypes at a specific location, with R = 0.95, 0.71 and 0.95, respectively (Fig. 6 A). Except genotypes 9, 16 and 17, other genotypes had higher dormancy levels but with lower correlation coefficient values between location effects and genotype effects, especially for highest dormant genotype 20.

The scatter plot distribution of Fig. 6 B indicates that locations 5, 8, 9 11 and 12 tended to reduce dormancy, and locations 1, 3, 6 and 10 tended to increase dormancy. The correlation coefficient (R) between location effects and genotype effects at the above locations was large and significant (positive or negative, R values in Fig. 6 B).

The amount of rainfall during ripening before harvest was positively correlated with the disposition to secondary dormancy, and the correlations became stronger with ripening period, while temperature showed negative correlations with dormancy but without significance (Table 3).

Discussion

Dormancy of hybrid CL oilseed rape

This study revealed a similar dormancy level and dormancy variation for 15 hybrid CL OSR genotypes in the F_1 and F_2 generations to that of non-CL OSR in previous studies (PEKRUN et al., 1997; GULDEN et al., 2003; GRUBER et al., 2004b; SCHATZKI et al., 2013a, b). In the research of GRUBER et al. (2004b), a dormancy variation of 3–76% among 32 non-CL OSR genotypes was detected, as well as a smaller range of 8–56% in a set of 28 black-seeded winter OSR genotypes measured by SCHATZKI et al. (2013a). The strong correlation between F_1 and F_2 generations in dormancy indicated that the disposition to secondary dormancy of hybrid CL OSR is heritable and robust (Fig. 2), but the correlation coefficient (R) was slightly lower than that of previous studies (SCHATZKI et al., 2013a; WEBER et al., 2013). First, seed storage time between genotypes in the F_1 generation was different, during which the disposition to seed dormancy would decrease (GRUBER et al., 2004b); second, the decrease of disposition to dormancy induction with time might be

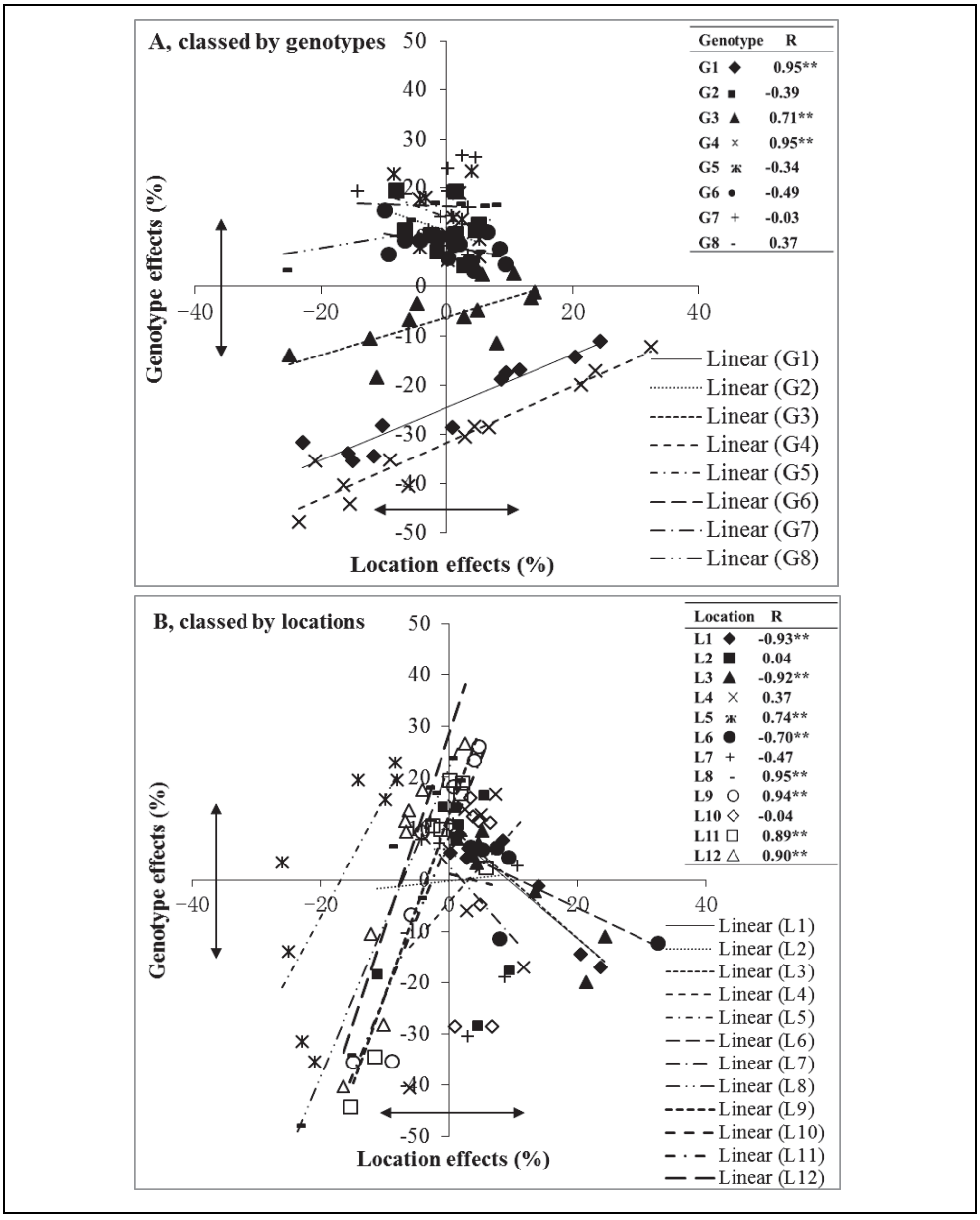

Fig. 6. Scatter plots of effects of genotype (A; n = 8) and location (B; n = 12) on the deviation of secondary seed dormancy (% dormant seed/viable seed after dormancy induction in the laboratory) of oilseed rape from the respective mean values across all genotypes and across all locations; Germany, 2012. Genotype 9 and 10 are Clearfield (CL) oilseed rape hybrids; genotypes 16 21 are non-CL hybrids. X-axis: deviation of the dormancy of a genotype at a specific location from the mean across all locations (indicating location effects); Y-axis: deviation of a genotype at a specific location from the mean across all genotypes on that location (indicating genotype effects).
Effekte von Genotyp (A; n = 8) und Standort (B; n = 12) auf die Abweichung der sekundären Dormanz (% dormante Samen/lebensfähige Samen nach Dormanzinduktion im Labor) in Rapssamen vom jeweiligen Mittelwert über alle Sorten bzw. über alle Standorte; Deutschland, 2012). Genotypen 9 und 10: Clearfieldraps-Hybriden, 16–21 nicht-Clearfieldraps. X-Achse zeigt Abweichung der Dormanz eines Genotyps an einem spezifischen Standorts von seinem Mittelwert über alle Standorte; Y-Achse zeigt Abweichung der Dormanz eines Genotyps an einem spezifischen Standort vom Mittelwert aller Genotypen an diesem Standort.

Table 3. Correlations between secondary dormancy of eight winter oilseed rape genotypes and average rainfall or air temperature (2 m) at different periods of ripening across 12 locations in Germany (weather data from DWD, 2014). * significant at $P < 0.05$, ** $P < 0.01$
*Korrelationen zwischen der Dormanzneigung von acht verschiedenen Winterraps-Genotypen und dem durchschnittlichen Niederschlag bzw. der Lufttemperatur (2 m) an unterschiedlichen Terminen während der Samenentwicklung an 12 Standorten in Deutschland (Wetterdaten nach DWD, 2014). * P < 0,05, ** P < 0,01*

	April	May	June	July	Aug.	June–July	June–Aug.	July–Aug.
Rainfall	0.06	−0.18	0.36	0.68*	0.60*	0.62*	0.72**	0.78**
Air temperature	−0.26	−0.41	−0.22	−0.34	−0.36	−0.28	−0.34	−0.40

different between genotypes of this study compared to previous studies; and third, the seed coating of genotypes 7–15 in the F_1 generation might have influenced dormancy induction and germination rates during the dormancy test. Overall, the strong genetic background to seed dormancy indicated that the dormancy level in the

F_2 generation which can cause volunteer problems can be determined through analyzing the dormancy potential of the F_1 generation (seeds to be used for sowing).

In spite of the strong correlation in dormancy between mixed-IP and non-isolated seeds (Fig. 4), the dormancy values of non-isolated seeds in most of studied hybrid CL genotypes were lower than that of mixed-IP seeds, especially for the high-dormant group. Outcrossing via pollen between genotypes might have caused the difference in dormancy between isolated and non-isolated seeds. Moreover, the potential effects of microclimate in the perforated plastic bags in the flowering period have to be taken into account. Hence, experiments using male sterile plants could quantify effects of outcrossing on dormancy variation.

Based on plant-to-plant dormancy variation within genotype, the dormancy segregation in the F_2 generation was obvious (Fig. 5), in accordance with findings of WEBER et al. (2013). The phenomenon of individual plants with different dormancy levels in their offspring is probably not only a segregation in the F_2 generation because WEBER et al. (2013) found this heterogeneity also in offspring from open pollinated varieties. The dormancy variation within the offspring seemed to depend on genotype: the mean range of dormancy variation across high dormant genotypes (no.14 and 15 except 10) was smaller than that of low dormant genotypes (no. 3, 8, and 9; 34.9% *vs.* 44.4%); the largest plant-to-plant variation (19.1–90.9%) was found in genotype No.10 with medium dormancy level (62.6%) in the F_2 generation. The limited number of genotypes does not yet allow stating a clear correlation between mean level of dormancy and segregation in the F_2. We hypothesize, however, that high dormant OSR genotypes are stable in their disposition to dormancy, and the range of dormancy in their offspring is smaller than in medium or low dormancy genotypes.

According to the similar results for the levels of dormancy in non-CL OSR in previous studies and in CL OSR in this study, soil seed bank and volunteer emergence of hybrid CL OSR are supposed to be similar to that of non-CL OSR. The very low-dormant genotypes identified in this study would probably result in low numbers or even no volunteers, if all other agricultural practices such as soil tillage are performed in an optimal way. Meanwhile, the large dormancy variation between and within genotypes could offer breeders strategies to select and breed low dormant CL OSR in coming years.

Impacts of maternal environment on dormancy disposition

Maternal environment is supposed to influence dormancy disposition of OSR during seed formation and maturation (GULDEN et al., 2004a; GRUBER et al., 2009; WEBER et al., 2013; POSTMA and ÅGREN, 2015). This was corroborated by the current study, e.g. the mean dormancy value across genotypes harvested at IHO was higher than that at Hohenheim in field trial 1. The most evident difference between two locations in trial 1was the high rainfall at IHO in July (Fig. 1) in the last period of ripening, which might be responsible for the different mean dormancy levels. The same phenomenon was observed in trial 2, e.g. locations with high rainfall during seed ripening had plants with higher dormancy level (significant correlation, Table 3).

The effects of locations, genotypes, and their interaction (Fig. 6) also indicate that seed dormancy of low dormant genotypes seems to be more prone to be influenced by maternal environment. Generally, there seem to be locations where maternal environmental conditions during seed maturation can result in higher disposition to dormancy of OSR. The amount of rainfall in the last period of ripening seems relevant for the disposition of OSR seeds to dormancy. Maybe wet conditions during ripening trigger physiological mechanisms which would prevent seeds from pre-harvest sprouting. Experiments with and analysis of phytohormones such as abscisic acid, which is clearly involved in the physiology of OSR dormancy (GULDEN et al., 2004b; FEI et al., 2009), would help to better understand the development of dormancy. Additionally, growing OSR plants under varied but controlled conditions of irrigation and temperature, for instance in climate chambers, would allow identifying environmental conditions which are crucial for the disposition to dormancy during seed ripening of OSR.

Conclusion

Hybrid CL oilseed rape genotypes show dormancy levels similar to those of non-CL genotypes, based on the comparison to previous results. Selection of or breeding for low-dormant OSR seems feasible based on dormancy variability between and within genotypes, and based on the fact that dormancy values of the F_2 generation correspond to that of the hybrid F_1 generation, at least in the mean of the offspring. There exist locations that obviously allow higher segregation of the genotypes, so that low dormant genotypes can be more easily detected. It is still not known which maternal environmental factors actually influence the disposition to dormancy and what is the physiological background; precipitation seems to be one factor.

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