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Assessment of a set of rapeseed (*Brassica napus* L.) varieties under waterlogging stress at different plant growth stages☆

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Abstract – Rapeseed (*Brassica napus* L.) crop has a high yield potential in Morocco, particularly in the Gharb region. However, this area is subjected to relatively frequent water floods usually accompanied with soil waterlogging, which is harmful for the crop. This study aimed to assess the behavior and productivity of four Moroccan varieties under waterlogging stress conditions at four plant growth stages, against the control (absence of waterlogging). A field trial was carried out at the INRA experiment station of Allal Tazi during 2013/2014, and a pot experiment was conducted under shelter at the National School of Agriculture of Meknes during 2014/2015. The results obtained show that waterlogging stress significantly affected most of the studied parameters for all varieties and that germination and post-emergence seedling stages were the most sensitive to waterlogging stress conditions. Particularly, seed yield was drastically reduced for all varieties, and the reduction rate ranged from 19% for "INRA-CZH3" to 73% for "Narjisse" when waterlogging happened under rosette and young seedling stages, respectively. Overall, the variety "INRA-CZH3" presented the best agronomic performance and was the most tolerant to waterlogging occurring at different plant growth stages. Therefore, we recommend cultivation of this variety in the Gharb area. Its tolerance to such stress conditions is certainly attributed to its developed root system, its high seedling vigor and its large collar diameter. The two latter traits presented a high correlation with seed yield components and, thus, we recommend their use as selection criteria to breed for waterlogging rapeseed tolerance.

Keywords: rapeseed / waterlogging stress / plant stage / tolerance / selection criteria

Résumé – Évaluation de certaines variétés de colza (*Brassica napus* L.) soumises à un stress de stagnation d'eau à différents stades de croissance de la culture. La culture de colza (*Brassica napus* L.) possède un potentiel de rendement élevé au Maroc, notamment dans la région du Gharb. Cependant, cette zone est fréquemment exposée à des inondations, généralement accompagnées d'engorgement de sol, ce qui représente des conséquences néfastes pour la culture. L'objectif de cette étude a été l'évaluation du comportement et de la productivité de quatre variétés marocaines dans des conditions de stress de stagnation d'eau (liée à l'engorgement du sol) durant quatre stades de croissance des plantes, en comparaison au contrôle (absence de stress). Un essai au champ a été réalisé à la station expérimentale de l'INRA à Allal Tazi en 2013/2014 et un autre essai en pots a été réalisé sous abri à l'École Nationale d'Agriculture de Meknès en 2014/2015. Les résultats obtenus ont montré que le stress en question affecte de manière significative la plupart des paramètres étudiés, pour toutes les variétés, et que les stades de germination et de post-levée sont les plus sensibles aux conditions de stress. En particulier, le rendement en graines a été considérablement réduit pour toutes les variétés et le taux de réduction varie de 19 % pour « INRA-CZH3 » à 73 % pour « Narjisse », lorsque la stagnation d'eau se produit, respectivement, au stade rosette et stade jeune plantule. En général, la variété « INRA-CZH3 » présente les meilleures performances agronomiques et la meilleure tolérance à ce stress dû à l'engorgement ayant lieu à différents stades de croissance de la culture.

☆ Contribution to the Topical Issue "Rapeseed / Colza"
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Par conséquent, il est recommandé de cultiver cette variété dans la région du Gharb. Sa tolérance à de telles conditions de stress est certainement attribuée à son système racinaire développé, à la vigueur élevée de ses jeunes plantules et à son collet de grand diamètre. Les deux derniers caractères ont montré une forte corrélation avec les composantes du rendement en graines et, par conséquent, ils pourraient être utilisés comme critères de sélection pour l'amélioration de la tolérance du colza à l'excès d'eau plus ou moins prolongé au champ.

Mots clés : colza / stress de stagnation d'eau (engorgement) / stade de la culture / tolérance / critères de sélection

1 Introduction

Waterlogging occurs from the excess soil water and has a severe negative effect on crop growth and yield. Currently, because of climate change phenomenon, it becomes a major abiotic stress in large areas of the world (Jackson and Colmer, 2005). Under sustained flooding conditions, waterlogging causes a drop in oxygen availability to plants or oxygen deficiency (hypoxia or anoxia), which leads directly to roots system damage and indirectly to leaf wilting and chlorosis (Grassini *et al.*, 2007; Wei *et al.*, 2013). Long-term waterlogging has severe effects on the stem and root growth and may cause plant wilt and likely its death, depending on plant tolerance level and environmental conditions (Schaffer *et al.*, 2006). Under hypoxia conditions, there is a suppression of oxygen-dependent processes and an inhibition of carbon assimilation and photosynthate utilization. Likewise, the functional relationships, mainly internal transport of oxygen between roots and shoots, are affected (Chugh *et al.*, 2012). An oxygen deficiency may limit the crop growth because of alterations in metabolism and nutrient uptake, leading to the generation of reactive oxygen species (ROS) which causes oxidative stress. Also, waterlogging stress can cause drastic dry matter and seed yield losses in various crops (Gutierrez Boem *et al.*, 1996; Aschi Smiti *et al.*, 2003; Grassini *et al.*, 2007; Dickin and Wright, 2008).

Rapeseed is one of the most important oilseed crops in the world. In 2016, it reached a seed production close to 69 million tons, contributing by more than 12% of the global oilseed production, and ranking third after soybean and oil palm (FAOSTAT, 2018). The cultivation of rapeseed was introduced for the first time in Morocco in 1981. The crop has exhibited a good adaptation to different areas mainly those that are humid and sub-humid, such as Gharb area, in which the ever highest seed yield (4 t/ha) was obtained in a field yield trial (unpublished data). However, the Gharb area is quite rainy, with an annual average rainfall exceeding 500 mm, and is often subjected to relatively frequent water floods due to soil waterlogging. Thus, under such conditions, rapeseed as well as other several crops can be seriously affected.

Yield reduction in rapeseed could be observed after three or more days of flooding stress, depending on the climate and the plant growth stage, and are greater with winter than spring flooding (Gutierrez Boem *et al.*, 1996). However, Cannell and Belford (1980) found that yield was not affected by waterlogging of 10 to 42 days during vegetative stage, with very low temperatures. Under waterlogging stress, dry weight, shoots and roots length, plant height, leaf photosynthetic rate, superoxide dismutase (SOD), catalase (CAT) and peroxidase (POX) activities are reduced, whereas accumulation of leaf malondialdehyde (MDA), lipid peroxidation and ethylene production in the leaves are increased (Zhou and Lin, 1995; Habibzadeh *et al.*, 2012). Several studies on the effects of waterlogging on rapeseed were carried out in China, and just few ones were conducted in other countries of the world, such as UK (Cannell and Belford, 1980), Pakistan (Ashraf and Mehmoud, 1990), USA (Daugherty and Musgrave, 1994), Argentina (Gutierrez Boem *et al.*, 1996) and Australia (Zhang *et al.*, 2004). However, no study has been done in the Mediterranean area. Furthermore, reported findings regarding plant growth stages sensitive to waterlogging, are sometimes controversial from one study to another. In addition, only few researchers from China focused on the genotypic variation for waterlogging tolerance. They found varietal differences for waterlogging stress during seed germination and seedling stages (Chen *et al.*, 2006; Cheng *et al.*, 2010; Li *et al.*, 2010). In order to face the increased occurrence of waterlogging in various regions of the world, especially as a result of climate change, there is an urgent need to develop adapted varieties that can tolerate such conditions. In this regard, relevant and reliable selection criteria to use in rapeseed breeding programs should be identified. Therefore, the present research conducted in Morocco, a Mediterranean area, aimed to:

- investigate the effect of waterlogging on plant growth, physiology and productivity of four rapeseed varieties grown under waterlogging conditions occurring at different growth stages;
- determine the plant growth stages most sensitive to waterlogging;
- identify the varieties most tolerant to waterlogging;
- develop selection criteria to be used in breeding rapeseed varieties for tolerance to flooding.

The study was carried during two consecutive years, first under field conditions (2014), then in pots (2015). The field experiment was carried out in the Gharb area, characterized by leveled lands and soils rich in clay and silt, which promotes water stagnation after heavy rains and excessive irrigation. The pots experiment was conducted in order to confirm the field findings and to investigate more deeply the root behavior under waterlogging stress.

2 Materials and methods

2.1 Plant material

Four Moroccan rapeseed (*Brassica napus* L.) varieties developed by the National Institute of Agricultural Research (INRA) of Morocco were used in this study, namely "Narjisse", "INRA-CZH2", "INRA-CZH3" and "Lila". "Lila" is a synthetic variety while the other three varieties are inbred lines (Nabloussi, 2015). “Narjisse”, “Lila” and “INRA-CZH3” were registered in 2008, 2015 and 2018, respectively, whilst “INRA-CZH2” is still under evaluation for registration.

2.2 Waterlogging treatment

Plants grown in field and in pots were waterlogged to the soil surface for various days at different growth stages. Four treatment levels (T1 to T4) were considered. Under field conditions (2014), T1 corresponds to waterlogging stress applied directly after sowing during two 10-d spaced periods, each period consisting of 5-days water stagnation. T2 represents waterlogging stress occurring directly after emergence and through seedling stage, for three 7-d spaced periods in which plants were submerged during 5 days. Regarding T3, waterlogging stress was applied at rosette stage and was maintained for 7 days. Finally, T4 targeted floral bud stage during two 10-d spaced periods of 5-d water stagnation. In the case of the control treatment (T0), soil was kept drained, with no waterlogging stress, during the whole growth period.

Concerning the experiment conducted in pot, that was put under shelter to be protected from any rainwater, the same growth stages and waterlogging treatments were considered (T1, T2, T3, T4 and T0 as control). However, for each waterlogging treatment, water stagnation was maintained during only one 5-d period as planting was very late and plant growth speed in pot conditions was higher than that of field conditions.

2.3 Field and pot experiments

The experiment was conducted during two cropping seasons. In 2013/2014 season, the four varieties were evaluated at the INRA experimental station of Allal Tazi, located 30 km from Kenitra city (34°31’ N, 6° W) at an elevation of 10.5 m and with a rainfall average of 550 mm. Its soil is little evolved, with a vertic character and a clay-silty texture, having an average composition of 39% in clay and 34% in silt. This soil is considered, therefore, as hydromorphic. Planting was done on 28 November 2013 using a split-plot design with two replications. The experimental unit consists of 4 rows 3 m long, with 0.60 m row spacing. Waterlogging treatment was used as the main plot and variety as the sub-plot. Crop management was done according to the conventional cultivation technique adopted at the experimental station. Plants were harvested on 22 May 2014.

In the second cropping season (2014/2015), the four rapeseed varieties were evaluated in the greenhouse at the National School of Agriculture of Meknes. Planting was done on 26 February 2015 in pots (6 L capacity) filled with 5 kg of substrate consisting of dry sand and peat. To ensure waterlogging, the pots were placed inside other larger pots (12 L capacity) filled with a layer of gravel at the bottom in order to maintain water stagnation. Water was freely circulating between large and small pots to allow waterlogging conditions for germinating seeds and plants. The experiment was conducted using a complete randomized blocks design, with three replications. Regardless of the waterlogging stress applied at various growth stages, plants were properly fertilized, irrigated and treated against aphids to avoid other abiotic or biotic stresses.

2.4 Parameters measured

Data were collected on morphological, phenological, physiological and agronomic parameters in each experimental unit using four randomly selected plants for the field experiment and three randomly selected plants for the pots experiment. However, for seed oil content (SOC), just one measurement was done by variety for each waterlogging treatment. In the case of field experiment, seedling initial vigor (SIV) was evaluated at two leaves stage according to a grading scale from 1 (weakest vigor) to 5 (strongest vigor); plant height (PHT, cm), measured from the ground to the top of the plant at maturity; number of leaves per plant (NLP) at full flowering; number of principal branches per plant (NBP), determined at maturity; plant collar diameter (PCD, mm), measured at maturity using a calliper; root volume (ROV, mL), determined at full flowering by volume difference after and before soaking roots in test tube with water and root weight (ROW, g), determined at full flowering on washed fresh roots using a precision electronic balance. Phenological traits were flowering time (FLT, d) and maturity time (MTT, d), both evaluated at the variety level instead of the plant. FLT was determined as the number of days from emergence to flowering of 50% of plants of each variety, while MTT was the number of days between emergence date and the date when 50% of plants of each variety have reached the maturity. Physiological traits were chlorophyll content a (CAC, mg/g of dry matter) and chlorophyll content b (CBC, mg/g of dry matter), determined in accordance with Billore and Mall (1975), and proline content (PRC, mg/g of dry matter), determined according to Monneveux and Nemmar (1986). All these three parameters were evaluated on entirely developed leaves at full flowering stage. Agronomic traits, all measured at maturity, were number of pods per plant (NPP); pod length (PLE, cm); number of seeds per pod (NSP); thousand seeds weight (TSW, g), seed yield per plant (SYP, g) and seed oil content (SOC, % of dry matter), determined on intact whole seeds using nuclear magnetic resonance (NMR) method (Oxford 4000).

For the pots experiment, the physiological parameters CCA, CCB and PRC, the morphological root parameters ROV and ROW, as well as SOC were investigated. Furthermore, additional root related parameters, namely root length (ROL, cm) and adventitious roots weight (ARW, g), were included in the study in order to get a better understanding of the plant root behavior under flooding conditions. Physiological traits were measured at full flowering stage, whilst root parameters were determined during rosette stage.

2.5 Statistical analysis

Descriptive analysis, analysis of variance and analysis of correlations were performed using various procedures of the statistics software SAS (version 9.1.3) to test significant differences among varieties, waterlogging treatments and their interaction. Duncan’s new multiple range test was applied to compare the means at the 5% probability level.

Table 1. Analysis of variance (mean square and significance level of differences) for morphological, phenological, physiological and agronomic parameters of four rapeseed varieties evaluated under waterlogged field conditions at different plant growth stages (five treatments) during 2014.

Source of variation	Degree of Freedom	Parameters								
		SIV	PHT	NLP	NBP	PCD	ROV	ROW	FLT	MTT
Treatment (T)	4	11.65***	14095.30**	694.27**	42.15***	128.07***	1333.77***	652.35***	77.60***	110.40***
Variety (V)	3	10.40***	5273.55 ns	1150.09***	21.89***	48.54**	597.08*	225.41 ns	116.37***	36.53***
T × V	12	1.32***	4362.09 ns	197.50 ns	5.80 ns	20.77*	320.85 ns	220.18 ns	46.87***	40.53***

		CCA	CCB	PRC	NPP	PLE	NSP	TSW	SYP	SOC
Treatment (T)	4	1.40*	0.19 ns	99.04***	47048.05***	1.51 ns	25.02***	1.20***	477.08***	63.88***
Variety (V)	3	1.09*	0.35 ns	6.25 ns	14159.67*	1.32 ns	47.36***	0.75*	159.56**	20.54***
T × V	12	0.28 ns	0.20 ns	10.47 ns	4825.88 ns	1.72 ns	7.67 ns	0.58**	41.21 ns	26.67***

SIV: seedling initial vigour; PHT: plant height (cm); NLP: number of leaves per plant; NBP: number of primary branches per plant; PCD: plant collar diameter (mm); ROV: root volume (mL); ROW: root weight (g); FLT: flowering time (d); MTT: maturity time (d); CCA: chlorophyll content a (mg/g); CCB: chlorophyll content b (mg/g); PRC: proline content (mg/g); NPP: number of pods per plant; PLE: pod length (cm); NSP: number of seeds per plant; TSW: thousand seeds weight (g); SYP: seed yield per plant (g); SOC: seed oil content (%); *, ** and ***: significant at 0.05, 0.01 and 0.001 levels, respectively; ns: not significant.

3 Results

3.1 Climatic conditions

For field experiment, during the crop cycle, the minimum temperature was 5 °C, registered on December 2013, and the maximum temperature was 30 °C, recorded on May 2014. Cumulative rainfall throughout the crop cycle was about 365 mm, which was lower than the average of Sidi Allal Tazi location (550 mm), but was well-distributed throughout the different crop growth stages. These conditions were an advantageous for our experiment as no drought or natural waterlogging had occurred in any stage of crop growth, allowing us to apply waterlogging stress properly at the targeted growth stages.

3.2 Field waterlogging evaluation

3.2.1 Effect of waterlogging stage and variety on morphological parameters

Highly significant differences were observed among waterlogging stages for all parameters ($P < 0.001$), indicating that morphology of rapeseed plant was influenced by waterlogging stress and by the plant growth stage when this stress occurred (Tab. 1). Also, significant differences were found among the varieties studied for all parameters ($P < 0.05$), except plant height (PHT), indicating a genetic diversity among the tested varieties for these morphological traits. However, for all the parameters studied, except plant collar diameter (PCD), there was no significant effect of the interaction between waterlogging stages and varieties (Tab. 1). This showed that, with respect to those parameters, varieties reacted similarly to waterlogging stage.

In absence of waterlogging stress (T0 check), the mean seedling initial vigor (SIV) was 3, varying from 2 to 3.5 for the varieties "Narjisse" and "INRA-CZH3", respectively. This character was affected by waterlogging stress occurring in early growth stages, particularly during seed germination where the average SIV was reduced to 2 for all varieties. Interestingly, the variety "INRA-CZH3" maintained the highest SIV value for all waterlogging treatments (T1 to T4). Regarding PHT, the four varieties were comparable both in absence and presence of waterlogging. Nevertheless, this stress affected negatively PHT, mainly when it occurred after seedling emergence (T2), causing a 30% reduction compared to the check (from 152 to 111 cm). However, flooding stress occurring at floral bud stage (T4) did not affect PHT of all varieties and the observed mean value (160 cm) was even slightly higher than that recorded in absence of this stress (152 cm). This was particularly due to the increased height registered for the variety "Lila, (from 150 cm for T0 to 200 cm for T4). Regarding the number of leaves per plant (NLP) and the number of branches per plant (NBP), the varieties presented significant differences in presence as well as in absence of waterlogging stress and, overall, the variety "INRA-CZH3" exhibited the highest NLP (33 leaves) and the highest NBP (6 branches). Stage T2 proved again the most sensitive to waterlogging stress for plant leaves and branches. A 20% reduction was registered for NLP (31 leaves in T0 against 18 leaves in T2), whilst the NBP registered a 50% reduction (6 branches in T0 against 3 branches in T2). Similarly, PCD was also negatively affected by the waterlogging stress, decreasing from 16 mm, in absence of stress (T0), to 11 mm when the stress occurred during early seedling and plantlet development (T2), thus, confirming the high sensitivity of this stage to waterlogging. However, due to the significant effect of the interaction "waterlogging stage × variety" on this parameter, varieties reacted differently to waterlogging applied at different growth stages. Overall, PCD varied from 11 mm for "INRA-CZH2" to 15 mm for "INRA-CZH3", confirming the highest morphological performance of this latter under various waterlogging conditions. Regarding roots volume (ROV), a downward trend was registered from T0 to the successive waterlogging treatments (T1 to T4), and

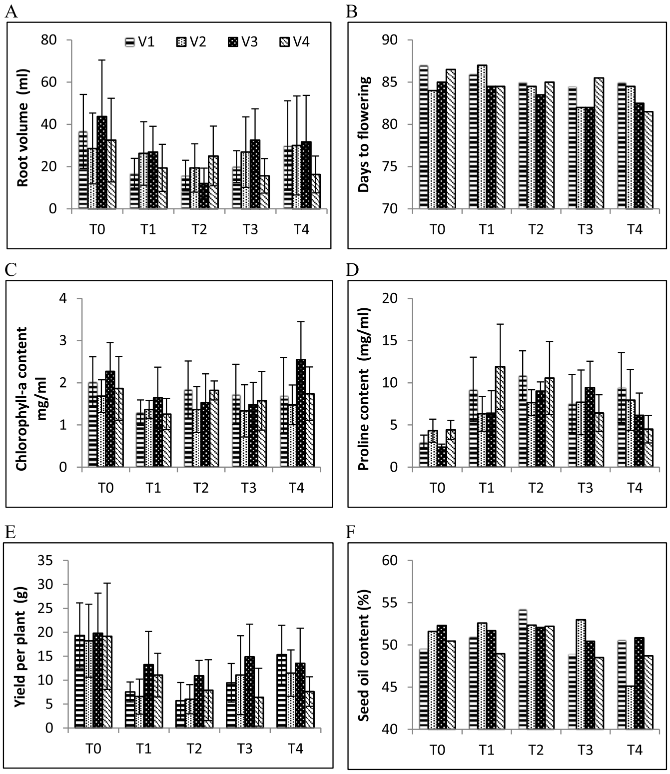

Fig. 1. Average treatment performance for each variety. A. Root volume. B. Flowering time. C. Chlorophyll-a content. D. Proline content. E. Yield per plant. F. Seed oil content. (V1: Narjisse; V2: INRA-CZH2; V3: INRA-CZH3; V4: Lila), (T0: absence of waterlogging; T1: waterlogging during germination; T2: waterlogging during post-emergence seedling stage; T3: waterlogging during rosette stage; T4: waterlogging during floral bud stage).

one could observe a fluctuation according to the treatment stage for each variety (Fig. 1A). As observed for the previous parameters, ROV was most affected in T2 waterlogging, indicating that this stage was the most sensitive to this stress. In absence of waterlogging, the variety “INRA-CZH3” presented the highest ROV (44 mL) and the variety “Narjisse” the lowest one (30 mL). However, under T2 waterlogging conditions, there was a sharp decline of ROV (73%) for “INRA-CZH3”, decreasing to 12 mL. Overall, for all waterlogging stages, “INRA-CZH2” and “INRA-CZH3” were comparable for ROV, registering the highest values (37 and 35 mL, respectively) (Fig. 2A). Similarly, roots weight (ROW) showed a downward trend from T0 to the successive waterlogging treatments. The drastic drop from 23 g in T0 to 12 g in T1 and T2 indicates that germination and early seedling stages were the most sensitive to waterlogging for this parameter. In absence of waterlogging, the variety “Lila” had the highest ROW (32 g) and the variety “Narjisse” had the lowest one (15 g). Under T1 waterlogging conditions, “INRA-CZH2” and “INRA-CZH3” maintained the highest ROW (14 g) compared to the other varieties, whilst under T2 waterlogging conditions, “INRA-CZH3” showed the lowest ROW (9 g). Nevertheless, this variety presented the highest overall average (25 g). Furthermore, it exhibited the strongest root density (0.97 g/mL) ever recorded for all waterlogging stages.

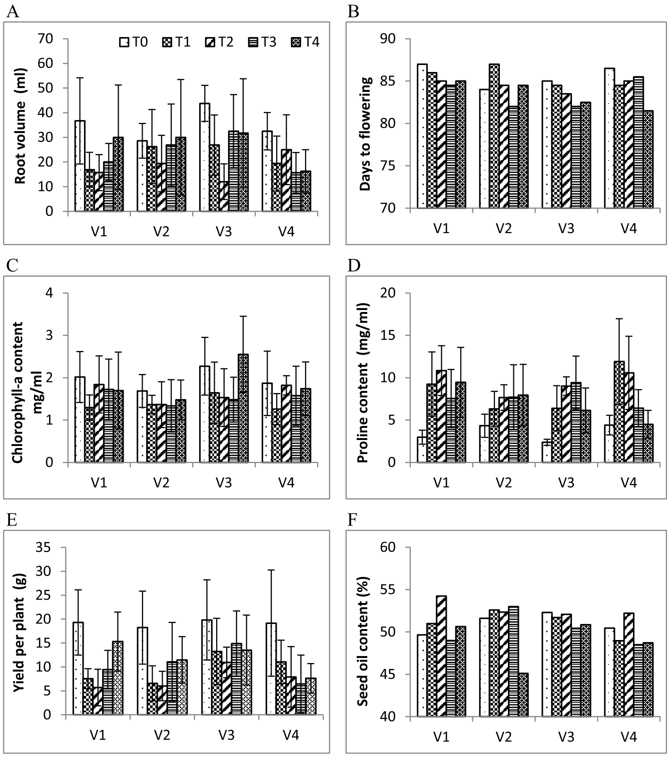

Fig. 2. Average variety performance for each treatment. A. Root volume. B. Flowering time. C. Chlorophyll-a content. D. Proline content. E. Yield per plant. F. Seed oil content. (V1: Narjisse; V2: INRA-CZH2; V3: INRA-CZH3; V4: Lila), (T0: absence of waterlogging; T1: waterlogging during germination; T2: waterlogging during post-emergence seedling stage; T3: waterlogging during rosette stage; T4: waterlogging during floral bud stage).

3.2.2 Effect of waterlogging stage and variety on physiological and phenological parameters

Highly significant differences were observed between waterlogging stages for all parameters ($P < 0.001$), indicating that physiology and phenology of rapeseed plant were influenced by waterlogging stress and by the plant stage under this stress (Tab. 1). Similarly, significant differences were also found among the varieties studied for all parameters, indicating a genetic diversity among the tested varieties for these physiological and phenological traits. Under drained conditions, the average proline content (PRC) was 3.82 mg/g, and this value increased in presence of waterlogging stress at different growth stages (Fig. 1D). The highest average PRC ever recorded, 8.46 mg/g, was observed for T2 conditions. Chlorophyll-a (CCA) and chlorophyll-b (CCB) contents dropped from 2 and 0.9 mg/g, respectively, under normal conditions (T0), to 1.14 and 0.52 mg/g, respectively, under rosette waterlogging conditions (T3) (Fig. 1C). These findings revealed that waterlogging stress during post-emergence and rosette stages was the most harmful for plant leaves, for all varieties studied.

The four varieties evaluated reacted differently to waterlogging for these two physiological traits. “INRA-CZH3” and “INRA-CZH2” accumulated the lowest PRC (5.58 and

Table 2. Correlation coefficients among morphological, phonological, physiological and agronomic parameters of four rapeseed varieties evaluated under waterlogging treatments at different plant growth stages in the field during 2014.

	SIV	PHT	NLP	NBP	PCD	ROV	ROW	FLT	MTT	CAC	PRC	NPP	NSP	TSW	SYP	SOC
SIV	–	0.212	0.431**	0.585**	0.571**	0.518**	0.578**	−0.277*	0.117	0.363**	−0.555**	0.462**	0.441**	0.118	0.512**	0.131
PHT		–	0.072	0.145	0.052	0.101	0.122	−0.116	−0.086	0.108	−0.249*	0.202	0.165	0.044	0.216	0.025
NLP			–	0.767**	0.678**	0.412**	0.354**	−0.110	0.034	0.348**	−0.296**	0.627**	0.325**	−0.050	0.668**	0.186
NBP				–	0.836**	0.429**	0.450**	−0.001	0.013	0.312**	−0.359**	0.715**	0.356**	0.061	0.751**	0.182
PCD					–	0.552**	0.540**	−0.027	−0.040	0.327**	−0.359**	0.664**	0.425**	−0.003	0.664**	0.277*
ROV						–	0.446**	0.133	−0.104	0.213	−0.291**	0.529**	0.305**	−0.002	0.530**	0.234*
ROW							–	0.061	0.001	0.357**	−0.482**	0.399**	0.355**	0.129	0.439**	0.186
FLT								–	−0.525**	0.012	−0.034	0.091	−0.083	0.016	0.056	0.224*
MTT									–	−0.234*	0.062	−0.081	−0.218	0.053	−0.048	−0.508**
CAC										–	−0.302**	0.199	0.279*	−0.010	0.214	0.322**
PRC											–	−0.392**	−0.227*	−0.094	−0.403**	−0.198
NPP												–	0.303**	0.980**	0.980**	0.345**
NSP													–	−0.078	0.392**	0.285*
TSW														–	0.148	−0.117
SYP															–	0.313**

[*] SIV: seedling initial vigour; PHT: plant height (cm); NLP: number of leaves per plant; NBP: number of primary branches per plant; PCD: plant collar diameter (mm); ROV: root volume (mL); ROW: root weight (g); FLT: flowering time (d); MTT: maturity time (d); CCA: chlorophyll content a (mg/g); CCB: chlorophyll content b (mg/g); PRC: proline content (mg/g); NPP: number of pods per plant; PLE: pod length (cm); NSP: number of seeds per plant; TSW: thousand seeds weight (g); SYP: seed yield per plant (g); SOC: seed oil content (%).

5.91 mg/g respectively) compared to "Narjisse" and "Lila" (6.73 and 8.14 mg/g respectively) (Fig. 2D). Similarly, "INRA-CZH3" produced the highest CCA and CCB contents (1.96 and 1.02 mg/g respectively), compared to the other varieties which ranged from 1.31 to 1.64 mg/g for CCA and 0.55 to 0.74 mg/g for CCB (Fig. 2C). These findings suggest that the variety "INRA-CZH3" might be the most resistant to waterlogging stress. In the case of phenological traits, the overall average FLT was about 86 d under drained conditions, but decreased under waterlogging conditions occurring mainly at rosette and floral bud stages to 83.50 and 83.30 d respectively, thus advancing flowering time by about 2.5 days (Fig. 1B). The variety "INRA-CZH3" was the earliest (83.6 d), regardless of waterlogging treatments, whilst the variety "Narjisse" was the latest (86 d) (Fig. 2B). Mean FLT varied from 81.5 d for "Lila" under T4 waterlogging to 87 d for "Narjisse" under drained conditions (Check). Besides, mean MTT was 144.4 d in absence of waterlogging and decreased when waterlogging occurred at early seedling growth stage to 141.6 d, while no significant variation was observed for the other growth stages. These findings show that only waterlogging occurring during early seedling growth stage advanced rapeseed maturity time. "INRA-CZH3" was the earliest maturing variety (143 d), regardless of waterlogging treatments, while "Lila" was the latest one (145 d). MTT varied from 135.5 d for "Narjisse", under T2 waterlogging, to 146 d for the same variety, under T0 conditions (Check), indicating that "Narjisse" was the most sensitive to T2 waterlogging stress that advanced maturity time by almost 10 days.

3.2.3 Effect of waterlogging stage and variety on agronomic parameters

Highly significant differences were observed among waterlogging stages for all parameters, except pod length (PLE) ($P < 0.001$), indicating that agronomic performance of rapeseed plant was significantly affected by waterlogging stress and the plant growth stage (Tab. 1). For agronomic traits, mainly number of pods per plant (NPP) and seed yield per plant (SYP), early seedling and plantlet stage (T2) was the most sensitive to waterlogging with induced reductions of these traits attaining 55 and 56%, respectively (Fig. 1E). This result shows that the sharp decline in seed yield is due to the drop in NPP. The variety "INRA-CZH3" exhibited the lowest reduction rate in NPP (39%) and in SYP (41%), indicating that it was the most tolerant to T2 waterlogging stress, compared to the other varieties. "INRA-CZH2" showed the highest reduction rate in NPP (69%) while "Narjisse" recorded the highest reduction rate in SYP (73%). Overall, and regardless of waterlogging stress conditions, the variety "INRA-CZH3" presented the best performance, exhibiting the highest SYP (13.42 g), compared to the other varieties (Fig. 2E). For TSW, the highest diminution rate (9%) was recorded under T1 waterlogging conditions. "INRA-CZH3" was the least affected variety, with only a 7% reduction rate, while "Lila" was the most affected, with a 10% reduction rate. Regarding SOC, the highest reduction rate was 4%, observed when waterlogging occurred at floral bud stage which seemed to be the most sensitive to such a stress for rapeseed oil content (Fig. 1F). With respect to the varieties studied, "INRA-CZH2" was the most sensitive, with 12.5% reduction, whilst "Narjisse" was the most tolerant with no SOC reduction. The variety "INRA-CZH3" showed 3% reduction. Overall and regardless of waterlogging stress conditions, the varieties "INRA-CZH3", "INRA-CZH2" and "Narjisse" presented the highest SOC (51.01%) compared to "Lila" (49.80%) (Fig. 2F).

Table 3. Analysis of variance (mean square and significance level of differences) for root and physiological parameters of four rapeseed varieties evaluated under waterlogged pot conditions at different plant growth stages (five treatments) during 2015.

Source of variation	Degree of freedom	Parameters							
		ROL	ROV	ROW	ARW	CCA	CCB	PRC	SOC
Treatment (T)	4	204.05^{***}	20.18^{*}	17.96^{*}	0.73^{*}	295.63^{***}	160.78 ns	0.88^{***}	7.00 ns
Variety (V)	3	29.46 ns	5.24 ns	4.43 ns	1.92^{***}	0.11 ns	165.35 ns	0.47^{*}	13.66 ns
T × V	12	74.80^{*}	9.40 ns	22.76^{***}	1.00^{***}	13.80 ns	216.19 ns	0.36^{*}	16.50 ns

ROL: root length (cm); ROV: root volume (mL); ROW: root weight (g); ARW: adventitious roots weight (g); CCA: chlorophyll content a (mg/g); CCB: chlorophyll content b (mg/g); PRC: proline content (mg/g); SOC: seed oil content (%); * and ***: significant at 0.05, and 0.001 levels, respectively; ns: not significant.

Table 4. Average treatment effect on rapeseed for some morphological, physiological and agronomic parameters evaluated under waterlogged pot conditions at different plant growth stages during 2015.

Parameters	Waterlogging treatments				
	T0	T1	T2	T3	T4
Root volume (mL)	6.21^{a}	5.63^{ab}	6.49^{a}	5.54^{ab}	4.54^{b}
Root weight (g)	5.45^{ab}	3.92^{c}	5.63^{ab}	6.07^{a}	4.22^{bc}
Root length (cm)	26.89^{bc}	24.25^{c}	28.75^{ab}	30.68^{a}	24.72^{c}
Adventitious roots weight (g)	2.89^{ab}	2.45^{c}	2.82^{ab}	2.97^{a}	2.61^{bc}
Chlorophyll content a (mg/g DW)	27.65^{a}	22.45^{b}	22.75^{b}	21.48^{b}	21.72^{b}
Chlorophyll content b (mg/g DW)	33.70^{a}	28.10^{a}	29.44^{a}	32.29^{a}	32.16^{a}
Proline content (mg/g DW)	0.157^{b}	0.234^{ab}	0.229^{ab}	0.342^{a}	0.167^{b}
Seed oil content (%)	39.95^{a}	39.17^{a}	38.51^{a}	39.09^{a}	37.89^{a}

For each parameter, mean values followed by the same letter are not statistically different ($P < 0.05$) according to DMRT.

3.3 Associations among the studied parameters

Table 2 shows the most important and significant correlations observed among some of the studied parameters in overall conditions of this study. Seed yield per plant generally exhibited weak correlations with most of the parameters. However, the most valuable one was recorded with seedling initial vigor, SIV (0.491). Similarly, SIV was also positively and significantly correlated with plant branching, NBP (0.585) and number of pods per plant, NPP (0.462), which are important seed yield components in rapeseed. This indicates that plants with high seedling initial vigor might have an interesting seed yield under normal and flooded conditions. In addition, there was a significant and negative relationship between SIV and PRC (−0.555), which revealed that stressed plants, accumulating high proline concentration in their cells, might have also weak seedling vigor. Furthermore, positive and strong correlations were observed between PCD and NBP (0.836), NLP (0.678), NPP (0.628) and SIV (0.571). This finding shows that, under different flooding conditions, plants with high PCD would be also characterized by a good leafiness, branching and pods productivity.

With regard to root parameters, root volume (ROV) and root weight (ROW) were positively associated to PCD and SIV, with important correlation coefficients ranging from 0.518 to 0.578. They were also negatively associated to PRC, with correlation coefficients of −0.391 and −0.482, respectively. Thus, plants with high ROV and ROW might accumulate less proline, indicating they were less stressed compared to those with lower ROV and ROW. Interestingly, these tolerant plants were also characterized by a high PCD and SIV. Chlorophyll a content (CCA) and chlorophyll-b content (CCB) were, in general, positively and moderately correlated to morphological and root parameters, namely NLP, NBP, SIV, PCD, ROV and ROW, with correlation coefficients ranging from 0.312 to 0.617. In the case of oil content, a very important trait for rapeseed production, a highly significant negative correlation is observed with maturity date, indicating that early maturing genotypes presented higher seed oil content.

3.4 Pot waterlogging evaluation

3.4.1 Effect of waterlogging stage and variety on root parameters

Analysis of variance revealed significant differences among waterlogging treatments for all root parameters studied (Tab. 3). However, varieties displayed significant differences only for adventitious roots weight (ARW), and were comparable for the rest of the parameters. The interaction "waterlogging stage × variety" showed significant differences for root length (ROL), root weight (ROW) and adventitious roots weight (ARW). This indicates that, the rapeseed varieties studied exhibited a differential response according to waterlogging stage.

The overall ROL average, all varieties and waterlogging stages combined, was 27.27 cm. Waterlogging stress, mainly occurring at post-emergence stage (T2) and at rosette stage (T3), induced a substantial ROL increase from 26.89 cm under drained conditions (T0), to about 29.50 cm under T2 and T3 waterlogging conditions. However, an important decrease was registered for T4 waterlogging to 24.72 cm (Tab. 4). In the absence of waterlogging stress, the variety "Lila" developed the highest root volume (30.50 cm), whereas "INRA-CZH3" presented the lowest one (23.94 cm). When waterlogging occurred during germination (T1), the variety "INRA-CZH3" developed the longest root (33.50 cm), while "Narjisse" produced the shortest one (21.56 cm). However, this latter

Table 5. Average rapeseed variety performance for some morphological, physiological and agronomic parameters under waterlogged pot conditions at different plant growth stages during 2015.

Parameters	Varieties			
	Narjisse	INRA-CZH2	INRA-CZH3	Lila
Root volume (mL)	5.83^{a}	5.43^{a}	5.18^{a}	6.19^{a}
Root weight (g)	8.83^{a}	8.00^{a}	7.97^{a}	9.80^{a}
Root length (cm)	27.31^{a}	26.69^{a}	26.80^{a}	28.10^{a}
Adventitious roots weight (g)	2.80^{ab}	2.59^{b}	2.79^{ab}	2.88^{a}
Chlorophyll content a (mg/g DW)	23.32^{a}	23.63^{a}	23.41^{a}	22.67^{a}
Chlorophyll content b (mg/g DW)	30.40^{a}	30.69^{a}	33.93^{a}	30.24^{a}
Proline content (mg/g DW)	0.211^{ab}	0.319^{a}	0.156^{b}	0.218^{ab}
Seed oil content (%)	38.94^{a}	37.60^{a}	39.93^{a}	39.32^{a}

For each parameter, mean values followed by the same letter are not statistically different ($P < 0.05$) according to DMRT.

registered the highest ROL under T2 and T3 waterlogging conditions (30.22 and 35.67 cm, respectively). Finally, when waterlogging was applied at floral bud stage, "Narjisse" developed the shortest ROL (22.11 cm), while "Lila" produced the longest one (28.83 cm). The varieties evaluated were comparable for ROV and ROW, with an average performance of 5.66 mL and 8.65 g, respectively (Tab. 5). However, a significant effect of waterlogging stage on these parameters was observed. For ROV, a downward trend was observed from T0 (6.21 mL) to T4 (4.54 mL), but there was a slight increase under T2 conditions (6.49 mL) (Tab. 4). Regarding ROW, it dropped from 5.45 to 3.92 g for T0 and T1, respectively, but increased to 5.63 and 6.07 g under T2 and T3 waterlogged conditions, respectively. This indicates that waterlogging occurring at post-emergence and/or rosette stages might even stimulate root development. This was possible because of the development of adventitious roots. In fact, there was an increase in ARW, reaching 2.97g when waterlogging happened at rosette stage (Tab. 4). However, waterlogging at germination stage caused the most important decrease in ARW (2.45 vs 2.89 g under normal conditions). The variety "Lila" presented the highest ARW average (2.88 g), while the variety "INRA-CZH2" exhibited the lowest performance (2.59 g) (Tab. 5). Under normal conditions (T0), "Narjisse" produced the highest ROW average (6.78 g) and the highest ARW (3.14 g), whilst "INRA-CZH3" was the lowest, with, 3.12 and 2.58 g, respectively. Under T1 waterlogging, ROW ranged from 2.20 g for "Narjisse" to 6.10 g for "Lila" and ARW fluctuated between 1.81 g for "INRA-CZH2" and 4.45 g for "INRA-CZH3". In the case of T2 waterlogging, the variety "Lila" developed the highest ROW (6.58 mL) and ARW (2.95 g), while "INRA-CZH3" had the lowest ROW (4.59 g), and "INRA-CZH2" produced the lowest ARW (2.65 g). For T3 waterlogging, the variety "INRA-CZH3" was found to be the most interesting, with an average performance of 6.96 and 3.06 g for ROW and ARW, respectively. Once again, the variety "INRA-CZH2" exhibited the lowest performance for these two root parameters (4.11 g for ROW and 2.79 g for ARW). Under T4 waterlogging conditions, "Lila" produced the highest performance for ROW and ARW (5.63 and 2.78 g, respectively), whereas "INRA-CZH3" produced the lowest performance (2.93 and 2.33 g, respectively).

3.4.2 Effect of waterlogging stage and variety on physiological parameters

Waterlogging stage had a significant effect on both proline (PRC) and chlorophyll-a (CCA) contents (Tab. 3). However, no significant difference was observed among the investigated varieties for all parameters. PRC increased from 0.157 mg/g under T0 to 0.342 mg/g under T3 (Tab. 4), indicating that plants having experienced waterlogging during rosette stage were more stressed compared to other treatments. However, Waterlogging at floral bud stage did not affect this parameter in comparison with the control conditions (T0). Similarly, waterlogging stress affected CCA which dropped from 27.65 mg/g, in absence of waterlogging, to an average of 22.60 mg/g, for (T1 and T2 waterlogging) and 21.60 mg/g for T3 and T4 treatments (Tab. 4). The four varieties reacted differently to waterlogging for PRC (Tab. 3). In fact, "INRA-CZH3" exhibited the best performance, (0.156 mg/g), while "INRA-CZH2" was the worst (0.319 mg/g). For CCA and CCB, these varieties were comparable (Tab. 3); however "INRA-CZH3" exhibited highest CCB average (33.93 mg/g), compared to an average of 30.44 mg/g for the three other varieties (Tab. 5). These results could indicate that the variety "INRA-CZH3" might be the most resistant to waterlogging stress, whereas the variety "INRA-CZH2" might be the most sensitive.

3.4.3 Effect of waterlogging stage and variety on seed oil content

Waterlogging application, in various plant growth stages, had no significant effect on seed oil content (SOC), even though there was a downward trend in SOC from T0 to T4 conditions (Tab. 4). In fact, SOC mean value declined from 40%, under drained conditions to 38%, under floral bud flooded conditions. The varieties studied were comparable for this parameter (Tab. 3). Nevertheless, slight differences were observed, with "INRA-CZH3" recording the highest oil content (40%) and "INRA-CZH2" the lowest (37.60%) (Tab. 5). The other two varieties showed intermediate oil content (39%).

4 Discussion

In general, waterlogging was harmful for rapeseed crop, affecting all the morphological, physiological, phenological and agronomic parameters studied, except pod length. Under field conditions, it was found that early seedling growth stage, after emergence and just before rosette stage, was the most sensitive to flooding for most of the studied parameters. In fact, SIV, PHT, NLP, NBP, PCD, ROV, ROW, MTT, NPP and SYP were markedly reduced and PRC was significantly elevated. This finding demonstrates that plants subjected to flooding in early seedling and plantlet growth stage were severely stressed and many important morpho-physiological and agronomic traits were seriously affected. Zhou and Lin (1995) working in China also reported that plant height, stem width, number of branches per plant, number of pods per plant and number of seeds per pod were significantly reduced by waterlogging at seedling stage. As a result, seed yield declined by 21.3% compared to the control. In our study, higher reduction (56%) was observed for seed yield, mainly due to the drastic decline in the number of pods per plant (55%). The difference in seed yield decline can be attributed to the nature and conditions of both experiments. Whilst our experiment was carried out under field conditions with flooding applied during three 5-d periods spaced by 7 days, Zhou and Lin (1995) used experimental containers in which plants were waterlogged for 30 days. Similarly, another research conducted in Argentina showed that winter waterlogging, coinciding with seedling stage, was particularly harmful for seed yield and its components, mainly branches per plant, pods per plant and seeds per pod (Gutierrez Boem *et al.*, 1996). However, in an old study on winter rapeseed conducted in United Kingdom, it was reported that early waterlogging in cold weather, during December/January, restricted leaf development and delayed flowering but did not affect seed yield (Cannell and Belford, 1980). Similarly, in a more recent research in Australia, Zhang *et al.* (2004) found that rosette waterlogging reduced leaf area index by 46% and shoot dry matter by 40%, but seed yield was 17% higher, in comparison with normal conditions. This is in disagreement with our findings that showed that, under rosette flooding conditions, both vegetative and agronomic traits were affected and seed yield was reduced by about 40%. This discordance may be explained by the difference in the stress intensity, the post-stress recovery conditions and the nature of plant material investigated (winter vs spring type and diverse varieties) in those environments. However, this decline remained lower than that observed under germination and early seedling growth (> 50%). It is evident from the literature that early seedling growth is highly sensitive to waterlogging in other crops (Sharma, 1994; Linkemer *et al.*, 1998; Zaidi *et al.*, 2004; Shahi *et al.*, 2006). Generally, flooding conditions induce some alterations in soil physico-chemical properties, such as pH redox potential and oxygen level. As a result, plants face a stressful environment in terms of hypoxia or anoxia, which adversely affect plant growth, development and survival (Ashraf, 2012). In fact, hypoxic conditions may cause drastic deficiencies of essential nutrients, such as nitrogen, phosphorous, potassium, magnesium and calcium in waterlogged plants (Smethurst *et al.*, 2005). Therefore, plants subjected to flooding exhibit marked yield losses. In addition, our study showed that flooding during germination affected negatively seedling initial vigor, root weight and TSW, whilst flooding at rosette stage restricted chlorophyll content and advanced flowering time. Regarding waterlogging occurring at floral bud, a slight reduction for time to flowering and oil content was observed.

The pots experiment confirmed that all root parameters studied, including ROW, ROL, ROV and ARW are decreased by flooding during germination and early seedling growth stages. However, the ARW and ROW performances observed under rosette waterlogging conditions were higher compared to the control conditions. In fact, it is commonly known that adventitious roots development takes place under flooding stress as a strategy of the plant to alleviate the stress hindering the basal roots (Ashraf, 2012). After deterioration of the main root system, the adventitious roots maintain the continuous supply of water and minerals to the plant (Mergemann and Santer, 2000; Dat *et al.*, 2006).

According to our investigation, significant decline of TSW was only due to waterlogging stress occurring during germination, which is in discordance with findings of Gutierrez Boem *et al.* (1996) who reported that spring waterlogging, coinciding with bud and flowering stages, reduced adversely the seed weight. However, the SOC reduction observed under floral bud flooding is in agreement with findings of Gutierrez Boem *et al.* (1996). Furthermore, our results show that flooding occurring at all growth stages significantly decreased leaf chlorophyll content, and that the greatest reduction, for both chlorophyll-a and −b, was observed for rosette stage flooding under both field and pots conditions. Zhou and Lin (1995) have also found significant decline in chlorophyll content by waterlogging at seedling and floral bud stages. Flooding is known to induce the destruction of chlorophyll in stressed plants and the decline in chlorophyll content affects directly or indirectly the photosynthesis capacity of these plants (Ashraf *et al.*, 2011).

Our results suggest that rapeseed was sensitive to excess moisture conditions, mainly during early seedling growth stage. Nevertheless, the results obtained also evidenced a genetic variation for its sensitivity or tolerance to this stress. Differential responses of the studied varieties were observed for all plant growth stages, with the variety "INRA-CZH3" being the most tolerant to waterlogging stress and, thus, presented the best overall performance. In fact, "INRA-CZH3" developed more main and adventitious roots to face such water stress conditions, and maintained a higher chlorophyll b content to ensure more photosynthesis, compared to the other varieties. Previous studies in China also reported varietal differences in tolerance to waterlogging stress occurring in seed germinating and seedling stages (Chen *et al.*, 2006; Cheng *et al.*, 2010; Li *et al.*, 2010). Similarly, genetic differences in tolerance to excess moisture were reported in many other crops such as wheat (Ding and Musgrave, 1995; Setter *et al.*, 1999), barley (Setter *et al.*, 1999; Pang *et al.*, 2004), maize (Zaidi *et al.*, 2004; Anjos e Silva *et al.*, 2005) and soybean (Van Toai *et al.*, 1994). Waterlogging-tolerant genotypes may have specific morphological and anatomical characteristics allowing their survival and functioning under waterlogging conditions, such as aerenchyma formation and adventitious root development (Laan *et al.*, 1989). In addition, under waterlogged conditions, some potential genes can exhibit an induced expression in low oxygen environment and, therefore, might be involved in conferring tolerance to such stress conditions (Ashraf, 2012). It was suggested that genetic basis of waterlogging tolerance in rapeseed, during the seedling stage, is complex as too many QTL are involved for some associated traits, such as plant height, root length, shoot dry weight and root dry weight, and for waterlogging tolerance coefficient (Zhen *et al.*, 2014). Recently, it was reported that adapted varieties might enhance their tolerance to waterlogging by regulating the genes involved in metabolism of endogenous hormones and protective enzymes (Zhang *et al.*, 2019). Among these hormones, abscisic acid (ABA) might play an important role in rapeseed tolerance to waterlogging (Zou *et al.*, 2015).

Considering the associations among the studied parameters, and with regard to the characteristics of the variety "INRA-CZH3", which proved to be the most tolerant and best performing under waterlogging stress conditions, one could suggest that seedling initial vigor and plant collar diameter, (easily observable morphological parameters in the field), can be considered as very promising selection criteria to be used in rapeseed breeding program for tolerance to excess moisture. Seedling vigor may express the ability of such a seedling to rapidly elongate and emerge, after germination, to avoid and/or escape waterlogging or submergence stresses (Vu *et al.*, 2013). Previous studies had also reported that seedling initial vigor and collar diameter were found to be reliable indicators of good adaptation and performance of genotypes under various environmental abiotic stresses such as drought, heat, chilling and salt (Foolad and Lin, 2012; Liua *et al.*, 2012; Platten *et al.*, 2013; Houmanat *et al.*, 2016). Therefore, the adoption and use of these traits, as selection criteria, could allow the selection and development of adapted rapeseed germplasm with multi tolerance to various abiotic stresses, including waterlogging.

5 Conclusion

Rapeseed crop was found to be sensitive to waterlogging stress occurring, particularly, during germination and early seedling growth stages. As a result, a remarkable decline in seed yield was observed and could exceed 50%. However, the studied varieties reacted differently to this stress, and "INRA-CZH3" proved to be the most tolerant, exhibiting the best performance for most of the agronomic and physiological parameters investigated. Seedling initial vigor and plant collar diameter could be taken as selection criteria to breed rapeseed for tolerance to waterlogging stress. Further studies are necessary for a better understanding of the tolerance mechanisms of the variety "INRA-CZH3" under excess moisture stress conditions, and to investigate the genetic control and inheritance of tolerance to waterlogging stress in rapeseed.

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