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Simulated seawater flooding reduces oilseed rape growth, yield and progeny performance

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- **Background and Aims** Of the many threats to global food security, one of the most pressing is the increased incidence of extreme weather events. In addition to extreme rainfall, a combination of global sea level rise and storm surge is likely to result in frequent episodes of seawater flooding in arable systems along low-lying coasts. Our aim was to elucidate the effects of simulated seawater and freshwater flooding on the survival, growth and reproductive potential of four cultivars of the important seed crop, *Brassica napus* [canola, or oilseed rape (OSR)].
- **Methods** Established plants were exposed to 24 or 96 h freshwater or seawater root zone immersion (with a no immersion ‘control’). Initial post-treatment performance over 7 weeks was quantified using dry weight biomass. A second group of plants, cultivated until maturity, were used to quantify reproductive yield (siliqua and seed number, and seed size) and subsequent progeny performance (germination and seedling growth).
- **Results** Oilseed rape growth and reproductive responses were unaffected by freshwater, but seawater negatively affected growth and siliqua number for all cultivars, and seed mass for two (‘Agatha’ and ‘Cubic’). In addition to impacts on crop yield, the growth of seedlings cultivated from seed collected from maternal plants subjected to seawater immersion was also reduced.
- **Conclusions** Our results demonstrate the potential impact of seawater inundation on coastal cropping systems; although OSR may survive acute saline flooding, there are longer term impacts on growth and yield for some cultivars. The threat may necessitate changes in land-use practice and/or the development of salt-tolerant cultivars to maintain economically viable yields. In addition, by evidencing a hitherto unknown effect on reproductive performance (i.e. reduced seed yield) and subsequent seedling growth, our study highlights an important potential impact of coastal flooding on plant community dynamics for (semi-) natural habitats.

Key words: Flooding, food security, osmotic stress, salinity, sea-level rise, storm surge.

INTRODUCTION

Food security and climate change are two of the most pressing environmental issues facing the planet (Godfray *et al.*, 2010; IPCC, 2014). When combined, however, the increased food demand imposed by a growing human population coupled with global-scale shifts in temperatures, precipitation and sea-level rise will inevitably impose significant demands on agriculture (Parry *et al.*, 2005; Lobell *et al.*, 2008). Much of the environmental threat from climate change stems from acute extreme events rather than simply longer term chronic change alone (Rahmstorf and Coumou, 2011; Vasseur *et al.*, 2014; Parmesan and Hanley, 2015) and, of the former, flooding represents one of the greatest challenges. Future climate scenarios consistently predict major regional shifts in the intensity of extreme precipitation episodes across the globe and concomitant increases in large-scale regional flooding along river catchments (Li *et al.*, 2013; Singh *et al.*, 2013; IPCC, 2014). In addition to fluvial flooding, however, a combination of changes in sea-surface temperatures, weather patterns and sea-level rise is predicted to increase the frequency and severity of oceanic storm surges (Vousdoukas *et al.*, 2016; Vitousek *et al.*, 2017). The result will be that many low-lying coastal areas face an increased risk of seawater inundation over

coming decades (Nicholls and Cazenave, 2010; Hoggart *et al.*, 2014). When taken together, extreme precipitation, storm surge and sea-level rise are likely to cause significant flood risk to global agriculture and, as a result, understanding crop response to, and tolerance of, coastal flooding has become a research priority (Jackson and Ismail, 2015).

Although flooding can cause significant losses at any time of the crop production cycle, yields are most likely to suffer if flooding occurs during critical development stages (Rosenzweig *et al.*, 2001; Parry *et al.*, 2005). For the UK, for example, extreme winter and spring precipitation is projected to increase (Fowler *et al.*, 2010) at a time when many arable crops are establishing ahead of summer harvest. This is one reason why the severe, but localized, 2014 winter floods that affected only a small portion of southern England (14 000 ha) caused economic losses estimated at £6.9 million in arable systems alone (ADAS, 2014). Globally, severe freshwater and seawater flooding has long been identified as a significant economic problem for agriculture, and one that poses an additional regional threat to human nutrition (Page and Williams, 1926; Mirza, 2002; Chau *et al.*, 2015).

The impact of flooding on crop plants is well known, although research has almost exclusively focused on the effects

of freshwater inundation. Flooding typically causes soil anoxia, as O_2 is consumed without replacement, and the accumulation of various ions (Mn^{2+} , Fe^{2+} and S^{2-}) and compounds detrimental to plant growth, while submergence also denies plant tissues access to O_2 and CO_2 (Flowers and Colmer, 2008; Perata et al., 2011). All of these factors can limit crop growth and productivity significantly (Malik et al., 2001; Perata et al., 2011; Ren et al., 2014; Mutava et al., 2015). Due to its high salinity (typically about 35 g L^{-1} salt of which chloride and sodium contribute 19 g L^{-1} and 11 g L^{-1} , respectively), seawater flooding imposes additional osmotic and ionic stresses; the former limits the plant's ability to absorb water and the latter can result in toxicity through the accumulation of Na^+ and Cl^- in tissues (Munns and Tester, 2008). As a response, plants have adapted to avoid or lessen the impact of salt ions via the synthesis and accumulation of stress metabolites and the regulation of other tissue ions (i.e. K^+) to exclude or compartmentalize Na^+ and Cl^- and re-establish homeostatic function (Maathuis and Amtmann, 1999; Munns and Tester, 2008).

From the perspective of agricultural production, even if crop plants survive freshwater or seawater flooding, any impact on growth or reproductive potential is of concern. Our understanding of the effects of salinity on crop performance is, however, focused largely on soil salinization in arid cropping systems (Pitman and Läuchli, 2002; Albacete et al., 2008; Flowers et al., 2010), and only a handful of studies have examined how agriculturally important species respond to short-duration immersion in seawater. White et al. (2014) report how immersion in seawater for only 24 h resulted in the accumulation of Na^+ and Cl^- in leaves of the pasture crop white clover (*Trifolium repens*). A concomitant increase in two key organic solutes (proline and sucrose) to re-establish osmotic balance was also observed, but nonetheless flooded plants showed reduced growth and flowering potential. Interestingly, White et al. (2014) also found variation between the responses of three different ecotypes to seawater immersion, suggesting that the relative tolerance of one ecotype could be of value in producing flood-tolerant cultivars for cultivation in low-lying coastal pastures. The study of Sun et al. (2015) is the only one to look at effects of seawater immersion on arable crops, with their experiment focusing on the responses of 1-month-old plants of ten crop plants (six of which were Brassicaceae) to 24 h of seawater immersion. All crops were negatively affected by immersion, with two (cucumber and Chinese greens) suffering complete mortality and the remainder showing reduced growth. However, since plants were harvested only 2 weeks after immersion treatments were imposed, it is unclear what potential any of the surviving crops had for long-term recovery or whether other key aspects of the crop production cycle (flowering and fruit/seed production) were affected by flooding.

The aim of this study was to determine how exposure to simulated seawater and freshwater flooding affected both immediate growth and longer term reproductive performance of the widely cultivated crop canola, or oilseed rape (OSR; *Brassica napus* L.). Beyond gaining an understanding of the short-term impact of flooding on mortality and growth of established plants, we also test the hypothesis that impacts on reproductive potential and subsequent seedling performance vary across four different cultivars. Elucidation of these responses is important

for several reasons; OSR is grown primarily for seed yield and thus any impact of prolonged fluvial or seawater flooding on reproductive output has potential economic repercussions. In addition, establishing variation in growth and yield responses may help identify established genetic materials from which to develop flood/salinity-tolerant cultivars. A more general understanding of plant growth and reproductive responses to acute seawater flooding is also lacking in the literature (see Hanley et al., 2019), and no study to date has tested the hypothesis that progeny performance is affected by the exposure of parent plants to short-duration seawater immersion. Consequently, our study offers an important insight into the longer term impacts that this increasing environmental issue may have on natural, as well as agricultural, plant species and communities.

MATERIALS AND METHODS

Study species

Oilseed rape is a hybrid of *B. rapa* and *B. oleracea* (Chalhoub et al., 2014), wild forms of the latter being a coastal species with some natural salt tolerance (Snogerup et al., 1990). OSR is grown globally and its seeds are harvested to produce food and bioenergy oils, and for use as an animal feedstock. It accounts for 14 % (by area) of agricultural land use in the UK (Garthwaite et al., 2018), and major producers globally include the EU, Canada, India and China (USDA, 2015), regions likely to experience significant flooding events over coming decades (IPCC, 2014). The OSR cultivars used in these experiments were 'Cracker' (LS Plant Breeding, Impington, UK), 'Agatha', 'Astrid' and 'Cubic' (Grainseed Ltd., Eye, Suffolk, UK). All are commonly cultivated in the UK.

Plant cultivation

One hundred seeds of each cultivar were germinated in 90 mm diameter Petri dishes containing two layers of Whatman No. 1 filter paper moistened with 5 mL of distilled water, maintained in an incubator at $16.5\text{ }^\circ\text{C}$ on a 12:12 h light:dark cycle. On germination (radicle emergence), 70 seedlings per cultivar were transplanted individually into 50 mm diameter, 50 mm deep plastic pots containing John Innes No. 2 potting compost and grown on in a naturally lit greenhouse with weekly watering with tap water, until early November 2014. At this time, seedlings possessing at least the first true leaf (equivalent to OSR growth stage 1.1; Sylvester-Bradley, 1985), were re-potted into larger $110 \times 110 \times 120$ mm plastic pots containing John Innes No. 2 potting compost. Greenhouse temperatures during this cultivation period were: mean daily minimum = $10.4\text{ }^\circ\text{C}$ ($\pm 0.4\text{ }^\circ\text{C}$ s.e.); mean daily maximum = $25.7\text{ }^\circ\text{C}$ ($\pm 1.0\text{ }^\circ\text{C}$).

Effect of immersion on growth

When the plants were 67 d old (early December 2014), 12 individuals from each cultivar (OSR growth stage 1.3–1.6; i.e. emergence of third–sixth true leaves) were allocated at random to one of five treatment groups. These were 24 or 96 h immersion

in seawater (S_w) (collected from Plymouth Sound – electrical conductivity = 45.51 mS cm⁻¹ at 16.2 °C); 24 or 96 h immersion in deionized water (D_w); or a no-immersion control treatment. Although river floodplains can experience much longer periods of immersion, sometimes extending to several months (Van Eck *et al.*, 2004; Muchan *et al.*, 2015), in this way we simulated the average 1 d long seawater flooding event reported for low-lying UK coastline habitats and extended the period to the maximum reported flood duration of 4 d (Environment Agency, 2014).

We recognize that inundation following coastal storm surge or fluvial flooding events would be likely to result in full shoot submergence but, by immersing to pot level (in large plastic tubs), our approach allowed us to separate the effect of ionic imbalance in the root zone rather than the impact of oxygen deficiency caused by full immersion that both treatments would impose. Immediately after immersion, the pots were allowed to drain fully before being arranged randomly on a wire mesh-topped bench inside the greenhouse; the wire mesh allowed free drainage and prevented cross-contamination between treatment groups. The pots were watered to capacity (with tap water) 48 h after seawater immersion.

Eight plants per treatment/cultivar combination were retained inside the greenhouse; the remainder were positioned outside, on adjacent elevated mesh. For both sets of plants, each individual was positioned at random, 20 cm apart from its nearest neighbour in 1 m long rows separated by 30 cm to simulate the recommended field density for OSR cropping systems in the UK (HGCA, 2014).

Greenhouse plants were watered twice weekly for a further 56 d; temperatures during this phase of the experiment were 4.9 °C (\pm 0.5) minimum and 18.0 °C (\pm 0.6) maximum. Surviving plants (growth stages 2.0–2.3; i.e. the plant has a rosette growth form and an extended stem with internodes) from each treatment/cultivar group were harvested at 113 d old (late January 2015), cleaned of any adhering compost and oven-dried at 50 °C for 24 h. A Levene's test for homogeneity of variance across treatment and cultivar levels was negative ($F_{19,189} = 2.896$, $P < 0.001$) and biomass data were log₁₀ transformed, resulting in a positive Levene's test ($F_{19,189} = 1.335$, $P = 0.165$). Univariate general linear model (GLM) analyses were used to compare the results of experimental flooding on transformed biomass. Rather than classifying plants in different groups into two separate factors (water, D_w vs. S_w ; and time, 24 h vs. 96 h), which would decrease the power of the tests, contrasts were employed to evaluate specific differences between treatment levels (control, D_w 24, D_w 96, S_w 24 and S_w 96). In addition to the F statistic and its probability, we report effect sizes (η_p^2) and power at $P < 0.05$ (power_{0.05}).

Effect of immersion on crop yield and progeny performance

The four individual plants from each treatment/cultivar group positioned on elevated outdoor standing were grown to reproductive maturity in order to assess the effects of immersion on seed yield. Plants were exposed to natural weather conditions and watered (to capacity with tap water) only following prolonged dry periods. Since individuals were randomly arranged with respect to treatment and cultivar, they were able

to cross-pollinate and so resulting progeny were most probably hybrids between cultivars. Three plants ('Agatha' 24 h D_w ; 'Cracker' 96 h D_w ; and 'Agatha' 96 h S_w) died during this period. The main stems of plants were harvested in mid-June when most siliqua were fully ripened (growth stage 9.9). We quantified the total number of siliqua per plant and, from six (randomly selected) siliqua per plant, quantified seed number and mean individual seed mass per pod (averaging across all six replicate siliqua for each plant).

All seeds from each of the six sampled siliqua per plant were pooled. From these, 40 seeds were set to germinate in 90 mm diameter Petri dishes containing two layers of Whatman No. 1 filter paper moistened with 5 mL of deionized water, maintained in an incubator at 18 °C on a 12:12 h light:dark cycle. In addition to the three plants that died before harvest, a further two parent plants – 'Cracker' 96 h D_w and 'Agatha' 96 h S_w – failed to yield sufficient seeds for the germination/seedling growth trials. Petri dishes were checked daily for 14 d; on germination (appearance of the radicle), seedlings were counted and removed. Six seedlings from each Petri dish were retained, and planted into a 50 mm diameter pot containing John Innes No. 2 potting compost. These seedlings were grown in controlled conditions (15 °C on a 12:12 h light:dark cycle with daily watering to capacity) until 14 d old when they were harvested and oven-dried (at 50 °C for 24 h) to determine dry weight biomass.

Levene's tests of homogeneity of variances were significant for siliqua number ($F_{19,57} = 2.621$, $P = 0.003$), seed number ($F_{19,56} = 2.962$, $P < 0.001$) and seedling biomass ($F_{19,498} = 2.291$, $P = 0.002$), but did not show departure from homogeneity for seed mass ($F_{19,56} = 1.264$, $P = 0.244$). Logarithmic transformation of the former three homogenized the variance for siliqua number ($F_{19,57} = 1.304$, $P = 0.217$), but not for seed number ($F_{19,56} = 10.625$, $P < 0.001$) and seedling mass ($F_{19,497} = 3.289$, $P < 0.001$). Consequently, we present the results of GLM's hypothesis testing for (1) seed mass where the untransformed variable did not depart from homogeneous; (2) seed number and seedling mass where logarithmic transformation did not homogenize the variance; and (3) log siliqua number where logarithmic transformation resulted in variance homogeneity.

RESULTS

Effect of immersion on plant growth

'Treatment' had a significant effect on adult plant biomass, with a moderate effect size ($F_{4,189} = 17.71$, $P < 0.001$; $\eta_p^2 = 0.273$; power_{0.05} = 1; Fig. 1), and with the contrasts between control and each of the other four treatment levels significant only for S_w 96 (contrast = -0.339, s.e. = 0.066, $P < 0.001$). More specific comparison showed: (1) a negative contrast between both S_w treatments vs. control (contrast = -0.219, s.e. = 0.058, $P < 0.001$); (2) a small, but significant, positive contrast between D_w treatments vs. control (contrast = 0.114, s.e. = 0.057, $P = 0.048$); and (3) a then obvious positive contrast between D_w and S_w (contrast = 0.333, s.e. = 0.045, $P < 0.001$), highlighting the smaller size of plants immersed in seawater. Plant biomass did not vary between cultivars, but the cultivar effect size was small ($F_{3,189} = 1.85$, $P = 0.140$; $\eta_p^2 = 0.029$;

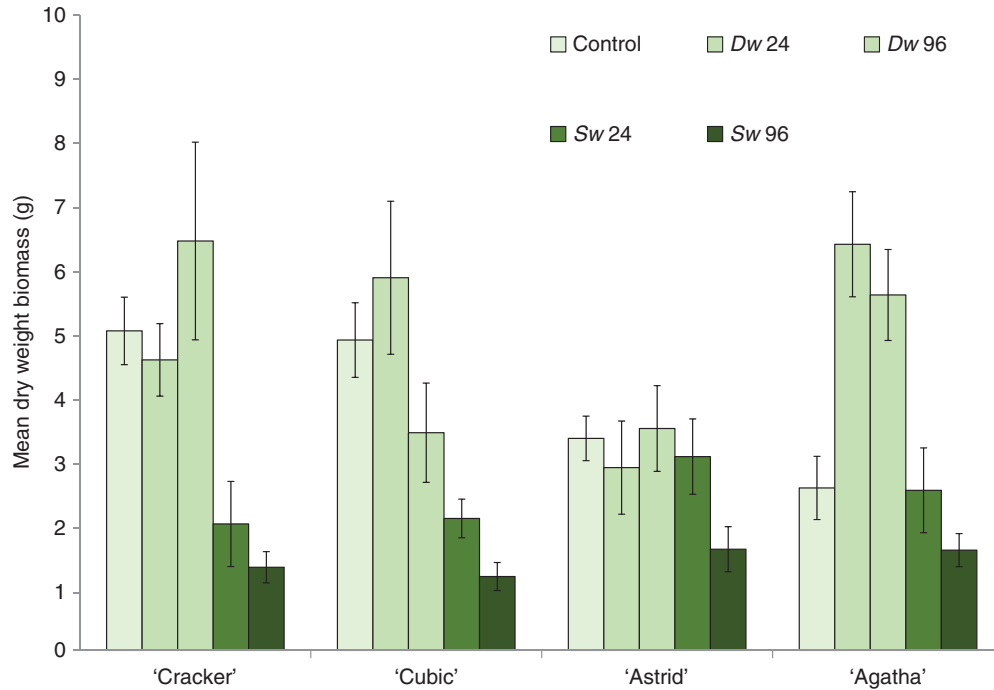


FIG. 1. The effect of root zone immersion in deionized water (*Dw*) and seawater (*Sw*) on mean (\pm s.e.) total above-ground dry mass of four oilseed rape (*Brassica napus*) cultivars ('Cracker', 'Cubic', 'Agatha' and 'Astrid') 2 months after plants (67 d old; growth stage 1.3–1.6) were subject to transient immersion (24 or 96 h with a zero hour control). $n = 8$ for all treatment/cultivar combinations.

TABLE 1. The effect of root zone immersion in deionized water (*Dw*) and seawater (*Sw*) on plant reproductive potential (crop yield) of four oilseed rape (*Brassica napus*) cultivars ('Cracker', 'Cubic', 'Agatha' and 'Astrid') 7 months after plants (growth stage 1.3–1.6) were subject to transient immersion (24 or 96 h with a zero hour control)

Treatment	Number of siliqua per plant				Seeds per siliqua				Seed mass (mg)			
	'Cracker'	'Cubic'	'Astrid'	'Agatha'	'Cracker'	'Cubic'	'Astrid'	'Agatha'	'Cracker'	'Cubic'	'Astrid'	'Agatha'
Control	Mean 35.5	29.8	22.0	35.8	13.2	22.4	22.3	20.3	0.04	0.08	0.07	0.06
	s.e. 8.6	2.8	2.4	4.8	2.7	1.2	1.0	1.2	0.009	0.009	0.004	0.005
24 h <i>Dw</i>	Mean 30.3	18.3	22.8	21.7	16.5	21.6	22.5	17.7	0.04	0.06	0.07	0.04
	s.e. 3.4	2.7	6.2	3.3	0.6	1.0	2.0	1.0	0.005	0.003	0.01	0.004
96 h <i>Dw</i>	Mean 40.7	28.0	28.8	27.5	11.4	25.0	20.9	19.9	0.03	0.07	0.06	0.05
	s.e. 13.2	3.6	2.7	5.0	4.9	0.5	1.1	1.4	0.02	0.004	0.005	0.004
24 h <i>Sw</i>	Mean 25.8	38.5	25.5	43.8	13.8	22.8	23.0	20.2	0.04	0.08	0.07	0.07
	s.e. 6.0	11.1	0.9	5.9	1.6	0.8	0.7	1.5	0.004	0.006	0.008	0.006
96 h <i>Sw</i>	Mean 24.3	11.5	17.5	14.0	13.6	19.4	22.5	9.2	0.03	0.04	0.07	0.02
	s.e. 6.2	3.2	3.0	5.1	3.2	2.0	1.2	4.7	0.01	0.006	0.006	0.01

$n = 4$ for all treatment/cultivar combinations except 'Cracker' 96 h *Dw*, and 'Agatha' 24 h *Dw* and 96 h *Sw* where $n = 3$.

power_{0.05} = 0.475). A significant 'treatment \times cultivar' interaction with moderate effect size ($F_{12,189} = 2.95$, $P = 0.001$; $\eta_p^2 = 0.158$; power_{0.05} = 0.989) emphasized several treatment- and cultivar-specific departures from the general trends described above ('Astrid' and 'Agatha', for example, were both tolerant of 24 h seawater immersion). No plants died during this first part of the experiment.

Effect of immersion on crop yield and progeny performance

The number of siliqua (Table 1) varied with 'treatment', with a small effect size ($F_{4,57} = 5.974$, $P < 0.001$; $\eta_p^2 = 0.295$; power_{0.05} = 0.978) but not by 'cultivar' ($F_{3,57} = 2.004$, $P = 0.124$;

$\eta_p^2 = 0.095$; power_{0.05} = 0.489), and there was no interaction ($F_{12,57} = 1.283$, $P = 0.254$; $\eta_p^2 = 0.213$; power_{0.05} = 0.643). The contrast analyses revealed a significant negative effect of *Dw* and *Sw* treatments compared with the control (contrast = -0.103 , s.e. = 0.050, $P = 0.046$), specifically highlighting lower siliqua numbers in *Sw* vs. control (contrast = -0.141 , s.e. = 0.055, $P = 0.014$). There was no variation between *Dw* and *Sw* (contrast = 0.76, s.e. = 0.046, $P = 0.105$) or *Dw* vs. control (contrast = -0.065 , s.e. = 0.056, $P = 0.250$).

Seed number per pod (Table 1) was not influenced by 'treatment' ($F_{4,57} = 2.206$, $P = 0.080$; $\eta_p^2 = 0.134$; power_{0.05} = 0.612) and, while varying between cultivars ($F_{3,57} = 20.265$, $P < 0.001$; $\eta_p^2 = 0.516$; power_{0.05} = 1), there

was no interaction with ‘treatment’ ($F_{12,57} = 1.31$, $P = 0.239$; $\eta_p^2 = 0.216$; $\text{power}_{0.05} = 0.655$). Mean individual seed mass (Table 1) did, however, vary according to ‘treatment’ ($F_{4,57} = 5.456$, $P = 0.001$; $\eta_p^2 = 0.277$; $\text{power}_{0.05} = 0.965$) and ‘cultivar’ ($F_{3,57} = 19.658$, $P < 0.001$; $\eta_p^2 = 0.509$; $\text{power}_{0.05} = 1$), although there was no significant interaction ($F_{12,57} = 1.799$, $P = 0.070$; $\eta_p^2 = 0.275$; $\text{power}_{0.05} = 0.822$). While contrasts highlighted that Dw and Sw had an overall difference from control (contrast = -0.009 , s.e. = 0.004 , $P = 0.036$), this was driven primarily by variation between Sw and control (contrast = -0.010 , s.e. = 0.004 , $P = 0.023$), and not by the difference between Dw and control plants (contrast = -0.007 , s.e. = 0.005 , $P = 0.122$). Interestingly, however, there was no variation between Dw and Sw (contrast = 0.003 , s.e. = 0.004 , $P = 0.373$). These results emphasize the different intensity of effects on different cultivars, i.e. ‘Agatha’ and ‘Cubic’ showed the most marked negative responses in the 96 h Sw treatment (Table 1).

Germination was unaffected by any of the immersion treatments imposed on parent plants (data not shown); the lowest germination for any one cultivar/treatment group was the 76 % recorded for seeds produced by ‘Cracker’ 96 h Sw (with three of four Petri dishes for this group nonetheless attaining >85 % germination).

Finally, seedling mass (Fig. 2) differed between treatments, with a small effect size ($F_{4,498} = 6.192$ $P < 0.001$; $\eta_p^2 = 0.047$; $\text{power}_{0.05} = 0.988$), but not among cultivars ($F_{3,498} = 1.874$ $P = 0.133$; $\eta_p^2 = 0.011$; $\text{power}_{0.05} = 0.486$), and there was a significant ‘treatment \times cultivar’ interaction also with a small effect size ($F_{12,498} = 2.295$ $P = 0.008$; $\eta_p^2 = 0.052$; $\text{power}_{0.05} = 0.959$). Contrast analysis revealed significant differences between control and Dw and Sw together (contrast = -0.004 , s.e. = 0.001 ,

$P < 0.001$), between control and Dw (contrast = -0.003 , s.e. = 0.001 , $P = 0.004$) and between control and Sw (contrast = -0.005 , s.e. = 0.001 , $P < 0.001$), but not between Dw and Sw (contrast = 0.002 , s.e. = 0.001 , $P = 0.089$). The significant interaction between the two main factors highlights differences in the intensity and direction of cultivar responses. The most affected, ‘Cubic’, displayed reduced seedling growth in both the 24 and 96 h treatments, while progeny collected from ‘Cracker’ showed no response to Sw immersion (Fig. 2). Seedlings grown from ‘Astrid’ and ‘Agatha’ parents exhibited reduced growth in the 96 h Sw treatments only, although, given the low parental replication for ‘Agatha’ (only two plants survived to reproduction), the apparent negative response for seedlings collected from this cultivar should be taken with caution.

DISCUSSION

Our results evidence substantial differences in OSR response to acute freshwater and seawater inundation; while the former exerted some impact on some of the responses examined here, the latter was more generally associated with reduced parent plant growth, seed yield and even progeny performance. As far as we are aware, this is the first time that the impacts of short-duration, acute, Sw flooding on several key growth and reproductive responses have been demonstrated across stages of the life cycle for any plant species. Indeed, the only previous study to examine this issue in arable crops, that of Sun *et al.* (2015), was limited to the immediate (2 week) post-immersion response, and while White *et al.* (2014) did look at growth and flowering in white clover over a 70 d post-immersion period, they did not

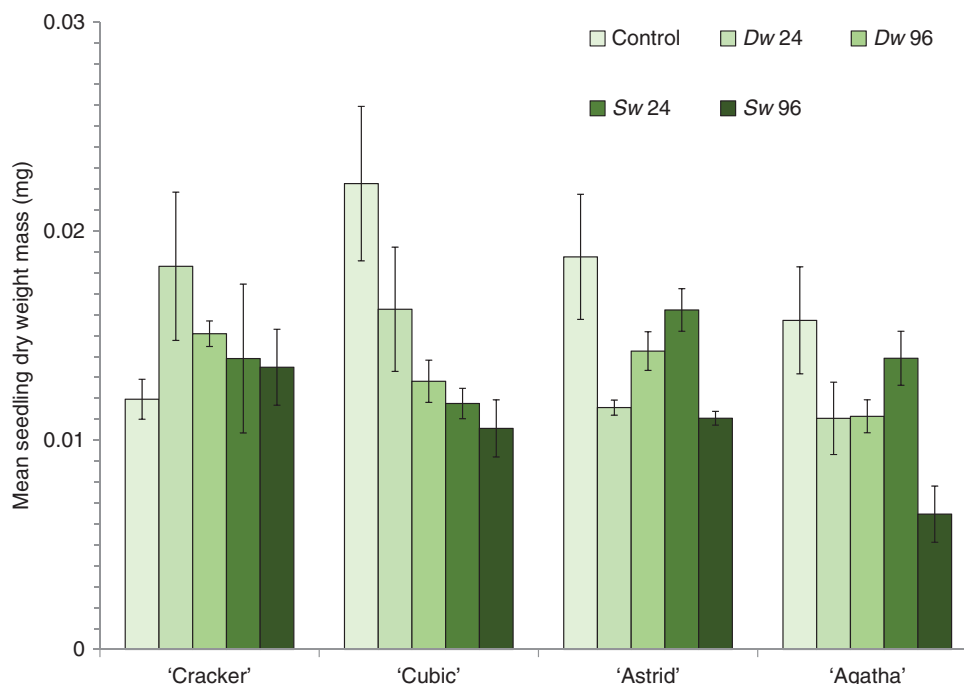


FIG. 2. The effect of root zone immersion in deionized water (Dw) and seawater (Sw) on mean (\pm s.e.) seedling dry mass of four oilseed rape (*Brassica napus*) cultivars ('Cracker', 'Cubic', 'Agatha' and 'Astrid') of plants grown from seeds collected from parent plants subject to transient immersion (24 or 96 h with a zero hour control, at growth stage 1.3–1.6). $n = 4$ for all treatment/cultivar combinations except 'Agatha' 24 h Dw where $n = 3$, and 'Cracker' 96 h Dw and 'Agatha' 96 h Sw where $n = 2$.

consider seed yield or progeny performance. While there was some variation between cultivars, this study shows that even transitory immersion in seawater has significant, consistent and long-lasting impacts on OSR crop yield. Indeed, the fact that reduced reproductive output (most notably siliqua number) was manifest 6 months after maternal plants were exposed to *Sw* immersion highlights the potential long-term impacts of seawater flooding on arable cropping systems.

The consequences of reduced seed yields on agricultural crops such as OSR are obvious, but our results also raise the possibility that wild plant species could suffer reduced reproductive success as a result of the effect of acute seawater flooding stress on seed development. It is well established that the maternal plant environment alters phenotypic expression in progeny (Herman and Sultan, 2011) and as such the reduced growth of seedlings from maternal plants subjected to *Sw* immersion reported here is unsurprising. Nonetheless, and while there is evidence that salinity stress can induce similar shifts in maternal provisioning and seedling performance [for example as shown in the grass *Cenchrus ciliaris*; Ruiz and Taleisnik (2013)], the fact that parent immersion in seawater for only 4 d can negatively influence subsequent seedling growth highlights more generally the impact of coastal flooding on plant community dynamics. Put simply, even if parent plants (of any native species) survive prolonged flooding, their later ability to contribute to the recovering community could be compromised. We know of no study to have demonstrated this response. For two of our maternal cultivars ('Cubic' and 'Agatha') where 96 h *Sw* immersion reduced mean seed mass by $\geq 50\%$, the most plausible explanation for the arrested growth of seedlings is that it resulted from reduced seed provisioning by the parent (Zas et al., 2013). We cannot, however, discount the possibility that other responses to salinity stress, including epigenetic changes, impact progeny performance and highlight this as a key area for future research.

From the perspective of arable plant species, progeny performance may be of minor importance however, since crops are routinely cultivated from commercially sourced seeds. Nonetheless, we demonstrated a consistent and marked reduction in siliqua number and seed mass for at least two cultivars ('Cubic' and 'Agatha') following 96 h *Sw* immersion, highlighting the significant economic impact that seawater flooding might have on coastal OSR crop yields. While a number of studies have shown that prolonged (i.e. one to several weeks) waterlogging reduces both OSR growth and yield (Cannell and Belford, 1980; Zhou and Lin, 1995; Xu et al., 2015), these studies looked at freshwater effects only. Although the relatively short-term *Dw* immersion treatments imposed here did not yield similar responses [but noting that we did not consider seed oil yield or content (Cannell and Belford, 1980; Xu et al., 2015)], all four cultivars exhibited much reduced plant growth, and later reduced siliqua number in the longer duration *Sw* treatment (see also Hanley et al., 2013). This highlights the challenge posed by salinity; even if a plant survives acute seawater immersion, it must prevent or alleviate damage caused by the accumulation of salt ions (Na^+ and Cl^-) in tissues. It is interesting that even the most prolonged immersion times (4 d) imposed here failed to induce mortality, a response that perhaps reflects an innate salinity tolerance due to OSR's heritage in *B. oleracea* and this parent species' natural affinity for maritime conditions (Snogerup et al., 1990). Salt tolerance is, however,

often accomplished by the accumulation of stress metabolites and the regulation of tissue ions to exclude or compartmentalize the potentially damaging Na^+ and Cl^- . Nonetheless even if successfully achieved, as seems to be the case here, there are costs in terms of subsequent plant growth and reproductive performance (Munns and Tester, 2008; White et al., 2014).

At a time of human population growth and economic development, there are increasing demands on food supplies but, when coupled with unpredictable and probably ever more extreme climate events, global food security is far from assured (Godfray et al., 2010; IPCC, 2014). Flooding is widely recognized as one of the key threats to arable crops, but most research emphasis is placed on pluvial, freshwater flooding where the major negative impact comes from soil anoxia. In the UK, the threshold for crop viability under this scenario is 15 d (ADAS, 2014) but, as we show here, by virtue of the added effect of salinity, seawater flooding of only 4 d duration can impact OSR yield (while the same duration under freshwater does not). Historically much of the global agricultural salinization problem stems from poor irrigation coupled with excessive evaporation and/or deforestation in hot, dry climates (Vinod et al., 2013). Nonetheless, sea-level rise and the expected increase in frequency and severity of storm surges (Vousdoukas et al., 2016; Vitousek et al., 2017) are likely to increase the risk of seawater inundation to temperate coastal arable systems (Nicholls and Cazenave, 2010). Under these conditions, farmers face a choice between changing land-use practice, or cultivation of flood-tolerant crops. There is a rich literature documenting salt tolerance in crops grown in regions where the problems of soil salinization are long established; indeed, for one of the most important, namely rice, crops grown near to coasts are frequently subjected to seawater intrusions, and a genetic capacity for salt tolerance has been identified (Ganie et al., 2014). The impact of seawater immersion demonstrated here for OSR, coupled with the increasing risk of seawater flooding for coastal agriculture globally, underscores a new impetus for research into salt tolerance in a wider range of arable crop species (Jackson and Ismail, 2015).

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