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Performance of ACCase-Resistant and ACCase-Susceptible Phenotypes of Sterile Oat *Avena sterilis* subsp. *ludoviciana* (Durieu) Nyman under Drought Conditions in the Greenhouse

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Abstract: Climate change might benefit water-stress-adapted weeds, further impairing their management. To evaluate the impact of soil moisture regimes on the growth and reproductive behaviour of ACCase-resistant and ACCase-susceptible phenotypes of sterile oat (*Avena sterilis* subsp. *ludoviciana* (Durieu) Nyman), a greenhouse experiment was carried out in 2020 and 2021. The factors were soil moisture regimes (100% field capacity (FC) as well-watered, 75% FC, 50% FC, and 25% FC) and ACCase-resistant and ACCase-susceptible phenotypes of sterile oat. Increased drought stress conditions reduced the number of tillers per plant by 34, 55, and 83% and the number of seeds per plant by 36, 61, and 89% in the 75% FC, 50% FC, and 25% FC conditions, respectively, compared to the well-watered treatment. Notably, both phenotypes reacted similarly to water stress, with no interactions between the two factors. Regardless of water stress, the resistant phenotypes produced fewer seeds per plant, indicating fitness costs. However, due to their high plasticity, both phenotypes will still produce seeds even when facing severe water stress conditions. Thus, sterile oat is expected to continue infesting crop fields in the near future, but with ACCase-resistant phenotypes being less successful than susceptible ones in the absence of herbicide application.

Keywords: drought stress; seed production; water regimes; herbicide-resistant phenotypes



Citation: Naderi, R.; Bijani, F.; Chauhan, B.S.; Mueller-Schaerer, H. Performance of ACCase-Resistant and ACCase-Susceptible Phenotypes of Sterile Oat *Avena sterilis* subsp. *ludoviciana* (Durieu) Nyman under Drought Conditions in the Greenhouse. *Agronomy* **2024**, *14*, 1268. <https://doi.org/10.3390/agronomy14061268>

Received: 29 April 2024

Revised: 29 May 2024

Accepted: 29 May 2024

Published: 12 June 2024



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1. Introduction

Sterile oat *Avena sterilis* subsp. *ludoviciana* (Durieu) Nyman is an annual grass and a dominant weed in winter cereals and rapeseed [1]. It is widely distributed across 55 countries, causing major yield loss in various crops [2,3]. It produces prolific amount of seeds that are difficult to separate from cereal grains [4]. Mahajan and Chauhan (2021) reported that sterile oat at the density of 16 plants m⁻² reduced wheat by 50% [5].

Acetyl-CoA carboxylase (ACCase) inhibitor herbicides have been widely used worldwide since their introduction in the late 1970s and 1980s to control grass weed species [6]. As a result, the herbicides rapidly selected, and are still selecting, resistant plants in grass weed species [7] and, thus, they have become the third herbicide group in terms of the frequency of resistance cases in the world [8]. This resistance in sterile oat has mainly resulted from a single amino acid substitution (isoleucine to leucine) in an enzyme at the herbicide site of action (Acetyl-CoA carboxylase; ACCase) that makes a change in the kinetics and function of the enzyme [7,9]. Herbicide-resistant weed species pose significant challenges in agroecosystems of both developed and developing countries, where herbicides remain the most economical method for weed management [10,11]. This is particularly true for broadcast cropping systems like winter wheat. The highest number of herbicide-resistant

weed cases have been observed in cereal crops, with wheat reporting the most instances, totalling 359 cases [8].

Wheat production in Iran occupies nearly 52% of arable land. Over the past 40 years, 108 herbicides with various modes of action have been registered in Iran, 28 of which are specifically for the selective control of weeds in wheat and barley. Significant resistance to ACCase-inhibiting herbicides has been observed in several weed species, including sterile oat, wild oat (*A. fatua* L.), littleseed canarygrass (*Phalaris minor* Retz.), hood canarygrass (*P. paradoxa* L.), and rigid ryegrass (*Lolium rigidum* Gaud.). Given the extensive wheat cultivation area and the continuous use of herbicides with only the ACCase inhibition mechanism of action, several regions of Iran are at risk of developing herbicide resistance [12]. In recent years, local farmers in Fars Province have claimed dissatisfaction with the effectiveness of clodinafop in controlling sterile oat. Despite its application, concerns persist regarding the inadequate management of sterile oat. The failure to achieve satisfactory control has prompted scrutiny and criticism from farmers, highlighting the urgency for more effective solutions in weed management practices within the region [13]. A decade of extensive use of ACCase inhibitor herbicides, such as clodinafop-propargyl, in major cereals in Iran after their introduction in 1994 has led to the evolution of resistance to ACCase inhibitor herbicides in sterile oat in wheat production regions of Iran such as in the Fars Province [13].

Water greatly affects sterile oat growth and development [14]. Recent research on weeds in response to climate change has suggested that focusing on drought-resistant weed biotypes is of great importance [15], as the different responses of herbicide-resistant and susceptible biotypes of a weed species to climatic changes may influence their fitness and population dynamics [16–18]. A better understanding of weed fitness under drought conditions could help in predicting the future population dynamics of herbicide-resistant weeds and their management [19]. Hassanpour-Bourkheili et al. (2021) investigated the germination response of ACCase-resistant (R) and ACCase-susceptible (S) sterile oat under various environmental conditions such as different temperatures, water potentials, NaCl concentrations, different pHs, darkness conditions, and burial depths [20]. They found no differences in the germination response between the R and S sterile oat plants under the aforementioned conditions. They concluded that the absence of a fitness cost at the seed germination level shows that controlling R sterile oats remains challenging, highlighting the importance of adopting crop and herbicide rotation to postpone the further evolution of resistance.

The increasing frequency of intricate extreme weather events presents a great challenge to the sustainability and reliability of agricultural production systems, as highlighted by Liu et al. [21]. These complex weather phenomena, characterized by their unpredictability and severity, jeopardize the resilience of agricultural practices and threaten consistent food supply. Weather patterns are changing due to increasing drought threats and enhancing global temperatures, which is having a detrimental impact on plant growth and productivity [22]. Drought tolerance in plants relies on modifying the photosynthetic system to changing conditions caused by water scarcity [23]. Drought stress affects all stages of photosynthesis, which include the function of photosynthetic pigments and photosystems, the electron transport chain, and the pathways for carbon dioxide reduction. Any disruption at these levels diminishes the overall synthetic capability of plants [24]. Drought stress significantly influences photosynthesis by reducing carbon dioxide diffusion and imposing metabolic constraints. The extent of this impact varies depending on the severity of drought stress, the presence of additional stress factors, and the species' ability to cope with such stressors [25].

Weed species adapted to a drought environment were found to be less adversely affected by climate change than those adapted to wet soil moisture conditions, and they were more competitive in dry soils [26]. Adaptation of weeds to water stress can lead to their further distribution and makes weed management increasingly difficult. Thus, a better understanding of the biology of weeds under water stress conditions could aid in developing better adapted weed preventative and management strategies [27]. Clearly,

awareness of the behaviour of herbicide-resistant weed phenotypes to field inputs, such as water, may help in managing herbicide-resistant weeds.

Several strategies are employed to effectively manage herbicide resistance. These include rotating herbicides with different modes of action and using herbicide mixtures, scouting and surveys, planting competitive crops, and adopting agricultural practices that enhance crop competitiveness, crop diversity, and crop rotations [28]. Various weed management strategies may provide effective control of sterile oat, but before designing such strategies, it is necessary to gain a better understanding of sterile oat phenotypes' responses to water regimes, as Iranian fields are increasingly facing drought conditions. A recent study revealed that sterile oat could survive and produce seeds at 40% of water holding capacity, suggesting that the weed is likely to be robust under drought stress conditions causing continued prominent reduction in crop yield [29]. However, there is limited information on the growth and seed production of ACCase-resistant and ACCase-susceptible phenotypes of sterile oat under a gradient of water stress conditions. Thus, the objective of our study was to determine the response of ACCase-resistant and ACCase-susceptible phenotypes of sterile oat to different water regimes.

2. Materials and Methods

To evaluate the impact of soil moisture regimes on the growth and reproductive behaviour of ACCase-susceptible and ACCase-resistant phenotypes of sterile oat, a greenhouse experiment was carried out in 2020 (January–May) and repeated in 2021 (January–May).

2.1. Plant Materials

Suspected acetyl-CoA carboxylase (ACCase) inhibitor-resistant sterile oat phenotypes (R) were collected from wheat farms of the School of Agriculture, Shiraz University, Shiraz, Fars Province, Iran. Susceptible phenotypes (S) were also collected from the same farms from fields, which never experienced herbicide application. Both phenotypes were collected from 12 sites and from each site 12 plants were collected, and seeds were pooled. Thus, these two groups were composed of several genotypes with the resistant phenotypes also being potentially composed of phenotypes with different resistance mechanisms. All sites were within a relatively confined geographic area and under the same general institutional management umbrella, except for the use or not of herbicides. As a result, there is minimal variation in environmental conditions, agronomic practices, and other factors that could potentially influence seed characteristics differently for the two phenotypes. ACCase resistance and susceptibility was confirmed in a greenhouse study, as described by Sasanfar et al. (2017) [30], in which plants were sprayed with different doses of clodinafop-propargyl. i.e., 0.5, 1, 2, 4, 8, and 16 L ha⁻¹. We acknowledge that it would have been ideal to use near-isogenic plant lines but unfortunately, they were not available. On the other hand, our approach reflects the actual situation of R and S phenotype compositions under field conditions, being relevant for their performance and subsequent management interventions. Thus, our pooled samples of each 144 plant individuals from 12 paired sites per phenotype captures a large and realistic genetic background, allowing us to compare the overall reaction of the two phenotypes to the water stress treatments. The experimental procedure is given in Figure 1.

2.2. Plant Growth Conditions

Seeds of both phenotypes of sterile oat were sown into 15 cm diameter × 30 cm tall plastic pots. In each pot, five seeds were sown and seedlings were thinned to three plants at the 3-leaf stage. The pots were filled with the top 30 cm of loamy-sand soil, which was collected from wheat–corn fields at the School of Agriculture, Shiraz University. Each pot was filled with 5 kg of soil.

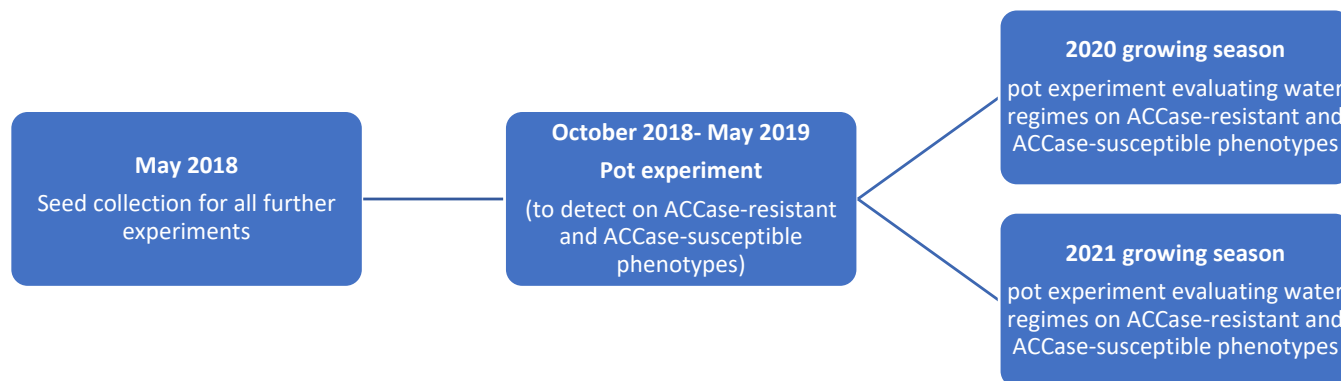


Figure 1. Flowchart depicting the experimental procedure.

The loamy-sand soil was air-dried, crushed, and passed through a 2 mm sieve before potting. The soil had a pH of 7.60, EC of 0.76 dS m^{-1} , total N of 0.21%, available P of 17 mg kg^{-1} , available K of 574 mg kg^{-1} , and 0.6–0.7% organic matter. The experiment was conducted two times. Seeds were sown on 11 January 2020 in the first experiment, and on 16 January 2021 in the second experiment. Greenhouse conditions were set at $24 \text{ }^{\circ}\text{C}/16 \text{ }^{\circ}\text{C}$ day/night, and 16 h photoperiod. The insecticide Confidor[®] was applied at a rate of $2 \text{ mL/L H}_2\text{O}$ three times during the experiment (tillering, stem elongation, and booting; stage 21, stage 30, stage 40, respectively, according to BBCH scale) to control for aphids.

2.3. Experimental Design and Treatments

Each experiment was conducted as a factorial arrangement in a completely randomized design with 8 pots (one replication) per bench in the greenhouse for a total of 24 pots (8×3 replicates). The first factor consisted of four soil moisture regimes (100% field capacity (FC) as well-watered, 75% FC, 50% FC, and 25% FC), which were applied after the three-leaf stage of plants through the pot weighing method [31]. The second factor included phenotypes, i.e., ACCase-resistant and ACCase-susceptible phenotypes of sterile oat. The field capacity of the pots was determined through saturating the soil of a pot with water. The saturated pot was covered with a plastic sheet in order to prevent evaporation and left to be drained from the bottom for 3 days. Pot weight was recorded after 3 days of drainage. The weight of soil moisture at field capacity was calculated as the difference between the soil weight after drainage and soil weight after oven drying at $105 \text{ }^{\circ}\text{C}$ for 24 h [31]. The pots were watered every 3 days.

Plants from each pot were harvested on 25 May 2020 in the first experiment and on 31 May 2021 in the second experiment as the seeds reached physiological maturity (characterized by yellow seed colour), oven-dried at $75 \text{ }^{\circ}\text{C}$ for 72 h, and weighed to determine aboveground biomass. Seeds were separated manually, cleaned, and counted, and seed yield per plant was measured. Plant height and number of tillers per plant were also measured before harvest. The measurements were taken for each plant separately and the mean of the three plants was calculated for each pot. The photosynthetic rate was measured on one randomly selected plant of each pot by using a photosynthesis device (LCi-SD Ultra Compact Photosynthesis System, ADC Bioscientific Ltd., Hoddesdon, Hertfordshire, UK). The PPFD was $400 \mu \text{ mol m}^{-2} \text{ s}^{-1}$ and CO_2 flow was $400 \mu \text{ mol mol}^{-1}$.

2.4. Statistical Analysis

Data obtained from the experiments were tested for normality, and subjected to analysis of variance (ANOVA) and means were compared with a Tukey's test ($p < 0.05$) using SAS (version 9.1, 2002; SAS Inc., Cary, NC, USA). Water regimes and seed types were considered fixed variables and years random variables. As the ANOVA indicated no significant ($p > 0.05$) differences between years for the effect of water regimes and seed

types on the measured traits, data from both years were combined. To estimate the effect of water stress on the different response variables measured, we performed a linear model for tillers plant⁻¹, number of seeds plant⁻¹, seed weight, total plant dry biomass, and photosynthetic rate, but a quadratic model for the effect of water stress on plant height was used, due to its better fit.

3. Results and Discussion

3.1. Number of Tillers and of Seeds per Plant

Soil moisture regimes significantly affected the number of tillers per plant ($p < 0.0001$) and the number of seeds per plant ($p < 0.0001$). Both traits were also significantly different between ACCase-susceptible and ACCase-resistant phenotypes ($p < 0.0001$, $p < 0.0001$, respectively). However, their interaction was not significant for both tillers per plant ($p = 0.529$) and seeds per plant ($p = 0.667$). Plants grown in the well-watered treatment had the highest number of tillers per plant (Figure 2a) and seeds per plant (Figure 2b). Increased drought stress conditions reduced the number of tillers per plant by 34, 55, and 83% and the number of seeds per plant by 36, 61, and 89% in the 75% FC, 50% FC, and 25% FC conditions, respectively, compared to the well-watered treatment. Water stress alters biomass allocation between roots and shoots. In water scarcity conditions, plants adapt by reallocating a greater portion of their photosynthesis output toward root growth. Consequently, it limits resources for leaves and reproduction. However, this strategy is crucial for plants to survive drought conditions [32,33]. A reduction in seed production due to enhanced water-stress levels has been reported in wild oat and sterile oat [29], *Echinochloa colona* (L.) Link [34], and *Amaranthus rudis* Sauer. [35]. Seed production is known as the most notable contributor to weed infestations. Our results suggest that sterile oat phenotypes could survive even at 25% FC, and produce sufficient seeds for re-infestation. These observations also revealed that in a drought environment, both phenotypes may continue expanding their range as a result of their ability to tolerate water stress. However, the higher reproductive ability of both sterile oat phenotypes at 100% FC indicates that they may predominantly infest irrigated crops. Their ability to produce seeds even under severe water stress conditions might make them able to enhance their invasiveness throughout Iran in crops suffering from drought stress, but also in fallow and dryland conditions [29].

Regardless of water regimes, ACCase-susceptible phenotypes had more tillers per plant (+71%) and number of seeds per plant (+55%) than the ACCase-resistant phenotypes (Table 1), indicating that the ACCase-susceptible phenotype has a greater potential for proliferation than the ACCase-resistant phenotype. Seed production is a vital fecundity trait that has effects on the population build-up [36]. Therefore, lower seed numbers produced by the ACCase-resistant phenotype would cause a reduced frequency of the resistance alleles in the absence of herbicide selection [37]. Hassanpour-Bourkheili et al. (2020) found increased seed production of imazamox-susceptible than resistant biotypes of wild poinsettia (*Euphorbia heterophylla* L.), suggesting a fitness penalty for the resistant phenotype [38]. However, investigating the germination response of ACCase-resistant and ACCase-susceptible sterile oat under different environmental conditions, Hassanpour-Bourkheili et al. (2021) reported no fitness cost for seed output [20]. Fitness costs associated with resistance to ACCase inhibitors have been reported to vary significantly among species, resistance mechanisms, the specific mutated allele conferring resistance, genetic backgrounds, experimental conditions (such as greenhouse or field settings), and competitive and non-competitive environments, as well as environmental conditions [39–41].

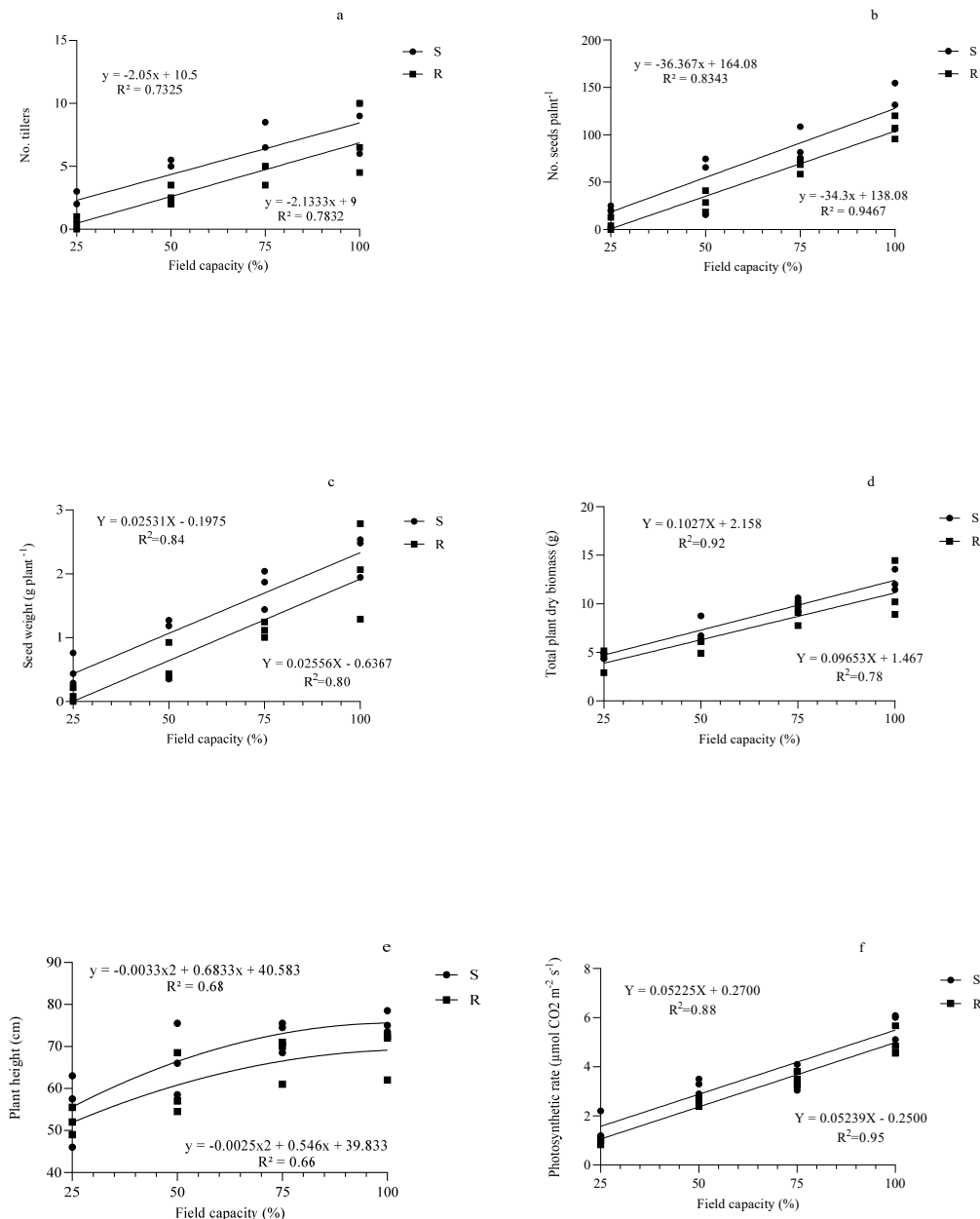


Figure 2. Effect of soil moisture on number of tillers plant⁻¹ (a), number of seeds plant⁻¹ (b), seed weight (c), total plant dry biomass (d), height (e), photosynthetic rate (f). Data were pooled across both years. S and R represent susceptible and resistant phenotypes of sterile oat, respectively.

Table 1. Number of tillers plant⁻¹, number of seeds plant⁻¹, seed weight plant⁻¹, and photosynthesis rate of susceptible and resistant phenotypes of sterile oat.

Phenotype	No. Tillers Plant ⁻¹	No. Seeds Plant ⁻¹	Seed Weight Plant ⁻¹	Photosynthesis Rate
Susceptible	6.04 ± 0.70 a	79.96 ± 10.2 a	1.54 ± 0.24 a	3.74 ± 0.27 a
Resistant	3.54 ± 1.01 b	51.54 ± 12.4 b	0.96 ± 0.20 b	3.01 ± 0.33 b

Means within the same column with the same letter are not significantly different ($p > 0.05$). Data were pooled across water stress treatments and both years (mean ± standard error).

3.2. Seed Weight per Plant

Seed weight per plant was affected by soil moisture regimes ($p < 0.0001$) and phenotypes ($p < 0.002$), but without a significant interaction ($p = 0.754$), indicating that both phenotypes responded similarly to water stress for this trait. Compared to the well-watered

treatment, reductions of 35% in 75% FC, 62% in 50% FC, and 89% in 25% FC conditions in seed weight per plant were observed (Figure 2c). The ACCase-susceptible phenotype showed significantly higher seed weight per plant (18%) than the ACCase-resistant phenotype (Table 1). Moderate-to-severe water stress decreases photosynthetic efficiency, reduces the duration of photosynthesis, accelerates leaf senescence, degrades plant structure, and impairs the transport of photosynthates to seeds [42].

3.3. Total Plant Dry Biomass and Height

Both total plant dry biomass ($p < 0.0001$) and height ($p < 0.001$) were affected by soil moisture regimes. Plants grown in the well-watered treatment showed 23, 45, and 63% greater dry biomass than those grown in the 75% FC, 50% FC, and 25% FC conditions, respectively (Figure 2d). The interaction of phenotypes and soil moisture regimes was not significant for either total plant dry matter and height ($p = 0.929$ and $p = 0.812$, respectively). Since both phenotypes produced lower biomass in severe moisture stress, it seems that water stress led to the reduction in fitness. However, even severe water stress used in this experiment could not completely inhibit the growth and seed production of the studied phenotypes. Plant height in 75% FC, 50% FC, and 25% FC conditions compared to 100% FC was reduced by 13, 12, and 24%, respectively (Figure 2e). The higher plant height of both phenotypes in the well-watered treatment compared to lower soil moisture levels could be due to the increased cell enlargement as a result of high turgor pressure in well-watered conditions [43]. It also has been reported that water stress adversely affects plant growth and development, primarily by reducing plant photosynthetic rate [44]. Similar results were obtained for wild oat and sterile oat in response to water stress in Australia, with greater height in the well-watered treatment and drastically decreased height as water stress increased [29]. Phenotypes had no significant effect on total plant dry biomass and height ($p = 0.879$ and $p = 0.106$, respectively).

3.4. Photosynthetic Rate

The photosynthetic rate was affected significantly by the soil moisture regime ($p < 0.0001$). The photosynthetic rate in the well-watered treatment was 29, 41, and 76% higher than in the 75% FC, 50% FC, and 25% FC conditions, respectively (Figure 2f). Phenotype had a significant impact on the photosynthetic rate ($p < 0.0001$), with the ACCase-susceptible phenotype having a higher photosynthetic rate than the ACCase-resistant phenotype (Table 1). The interaction of soil moisture regimes and phenotypes was not significant for the photosynthetic rate ($p = 0.4$). Plant productivity depends on photosynthesis, a process that requires water. The severity of drought stress determines the degree to which photosynthesis is inhibited. During drought stress, the diminishment in inorganic phosphate reserves in the Calvin cycle likely leads to reduced photosynthesis rates, which is due to the synthesis and accumulation of sugars [45]. Photosynthesis stands as the primary force behind seed yield and plant development, with fluctuations in photosynthetic pigment levels serving as crucial indicators of photosynthesis rates in plants subjected to drought stress. Previous research in wheat has highlighted that drought stress can lower leaf chlorophyll levels by 9%, consequently lowering the photosynthetic rate [46]. This significant alteration in plant physiology due to drought stress translates into reduced plant height, decreased growth rates, fewer tillers, lowered relative water content, diminished seed quality, and, ultimately, significant yield reductions [22]. Plants need to adapt their photosynthetic systems in response to environmental pressures [47]. The decline in photosynthesis due to water scarcity is closely linked to reductions in leaf water content and stomatal conductance [48]. Stomatal closure, occurring early on, serves as a defence mechanism to prevent excessive water loss via transpiration under mild-to-moderate drought stress [25]. Inadequate CO₂ availability triggers the oxygenase activity of Rubisco, leading to ATP loss [49]. Reduced utilization of light energy disrupts the electron transport chain [50], fosters the generation of reactive oxygen species [51], alters the ratio of photosynthetic pigments, and disrupts the organization of thylakoid

membranes [52]. Water stress can affect chlorophyll synthesis, the electron transport chain, and eventually the synthesis of all proteins and enzymes like carboxylase, which play vital roles in photosynthesis [53,54].

Investigating drought stress on three *Brassica* crops, Antunović Dunić et al. (2023) [23] reported that under drought stress, the tolerant variety's seedlings, Kale (*Brassica oleracea* L. var. acephala), did not display any outward signs of damage, with primary photochemical processes remaining undisturbed, and electron flow at the PSII level and intersystem electron carriers unaffected. Furthermore, the system's greater stability resulted in improved energy conservation through electron transport compared to Chinese cabbage (*B. rapa* L. var. pekinensis), and white cabbage (*B. oleracea* L. var. capitata). Although slight drought-induced disruptions were noted at PSI, these fully recovered following rehydration, indicating high drought tolerance. In contrast, Chinese and white cabbage experienced significant disturbances in PSII photochemistry under drought conditions.

The change in most of the measured parameters, i.e., tillers plant⁻¹, number of seeds plant⁻¹, seed weight, total plant dry biomass, and photosynthetic rate under different soil moisture regimes, best follows a linear model (see Figure 2a–d,f), while for the plant height, a quadratic model is a better fit (see Figure 2e).

Over the past few decades, drought has emerged as a major stressor significantly impacting plant development and crop yields. The successful establishment of weeds relies largely on their capacity to evolve stress tolerance, with weeds often demonstrating a greater ability to withstand stress compared to crops. Plants enhance their adaptability to thrive in dry environments primarily through the evolution of various mechanisms for drought escape, tolerance, and avoidance. Variations in drought tolerance among different plant species are primarily evident in terms of vegetative growth (plant biomass) and reproduction (number of seeds). Generally, weeds exhibit higher drought tolerance than crops, resulting in reduced crop yields and increased weed proliferation during drought years [55].

Soil moisture has a key role for weed establishment, growth, and reproduction [56]. Effects of water stress conditions on plants may depend primarily on plant species and the timing, extent, and period of water stress [57]. The potential of both phenotypes to produce seeds under drought stress could play a crucial role in affecting weed population dynamics under climate change conditions. The results of a recent study showed that Iran would be facing extended dry periods from 2025 to 2049 [58]. Since reduced water availability changes the competitive balance between crops and weed species, their response to drought is of great priority for weed management. Using more competitive crop cultivars [59] in drought stress conditions and manipulating crop sowing date [60–62] might also help in reducing sterile oat growth. Cultural practices, such as high crop densities or narrow row spacing, could further reduce sterile oat populations [29], but these management strategies should be lined up with agronomic strategies developed for water stress research programs.

4. Conclusions and Recommendation

The results of the present study indicate that the growth and reproductive traits of both ACCase-resistant and ACCase-susceptible phenotypes of sterile oat were greatly reduced under decreased water regimes as compared to well-watered conditions, but that they could remain troublesome under drought conditions by producing seeds. Regardless of water stress, the ACCase-resistant phenotype produced fewer seeds per plant and, thus, its spread and population build-up are expected to be reduced in the absence of herbicide pressure. To avoid further build-up of herbicide-resistant populations, cutting the tillers before crop harvest, especially in predominant resistant sterile oat populations also when densities are low due to drought stress, stimulating weed seed bank germination, and mechanical control during the fallow period could also be considered. A comprehensive understanding of the growth and reproductive behaviour of these phenotypes under water-stress conditions is essential to develop effective preventative and management tactics. Field studies to confirm our results, especially for growth characteristics such as tillers

per plant and seed production, will be needed to further justify the results and to develop specific management recommendations.

Author Contributions: Conceptualization, R.N., B.S.C. and H.M.-S.; methodology, F.B. and R.N.; formal analysis, R.N.; investigation, F.B. and R.N.; writing—original draft preparation, R.N.; writing—review and editing, R.N., F.B., B.S.C. and H.M.-S.; funding acquisition, R.N. and H.M.-S. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by Shiraz University, grant number 97GRC1M154663 to R.N and the Swiss National Science Foundation, project number 31003A_166448 to H.M.-S.

Data Availability Statement: The authors declare that the datasets are available from the corresponding author on request.

Conflicts of Interest: The authors declare no conflicts of interest.

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