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Review

How Can Weedy Rice Stand against Abiotic Stresses? A Review

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Abstract: Weedy rice is one of the most common weeds in rice cultivation in many rice areas throughout the world and it is able to cause significant yield reductions. Weedy rice is characterized by a high biological diversity that permits different populations to be identified on the basis of their morphological and physiological traits. This variability contributes to its success in different environments and allows different abiotic stresses, which are intensified by climate change, to be faced. Taller plants, enhanced tillering, seed shattering and the presence of red pericarp, variable hull coloration and awn morphology, linked to a deeper seed dormancy, are some of the traits that help weedy rice to spread in changing environments. The higher phenotypic plasticity and genetic variability of weedy rice make it more able to cope with temperature variations, intermittent water availability, soil salinity, drought conditions and increased CO_2 concentrations than cultivated rice. As these abiotic stresses will become more frequent in the future, weedy rice competitiveness may be higher, with a spread of infestations. Thus, the control of weedy rice should be based on an integration of different preventive and agronomic techniques, a sensible use of herbicides and the use of suitable rice varieties.

Keywords: morphological traits; physiological traits; temperature variations; salinity; drought; CO_2 increase; seed dormancy; herbicide resistance; integrated weed management

1. Introduction

Abiotic stresses, such as high temperatures, extreme weather conditions and an increase in carbon dioxide (CO_2), have been forecasted to occur much more often in the near future because of climate change [1]; these effects will in particular be more evident at low latitudes and in tropical regions, in which there is a high percentage of rice cultivation, and where most developing countries are located [2]. Moreover, in many areas in the world, crop production suffers from different abiotic factors that can occur locally, such as drought, low temperatures and salinity, which often occur concomitantly in a same area; the consequences of combined stress on plants are generally not comparable with the effect of a single stress at a time [1]. All these effects will have a huge impact on agriculture and, in particular, on rice production, as rice is one of the most frequently cultivated crops in many countries and is a staple food for the populations [3]. However, contradictory or inconclusive results have been found as to whether rice yields will decrease as a result of the pressure of different environmental factors [4,5]. The combination of abiotic stresses has the potential to affect rice yields, but also the growth of the most infesting weeds in rice production [1,6,7]. Even though rice crops are able to adapt to moderate environmental variations, crop production is often decreased or even completely hampered in the case of the persistent occurrence of different abiotic stresses, as crops have a limited ability to react, mainly because of their low genetic diversity [8]. Weeds are also undergoing the same environment changes as the crops, but they are in general more adaptable both because of the higher genetic diversity of the different populations and because of their greater phenotypic plasticity, which is the ability of a genotype to show multiple phenotypes in response to different environmental variations [8,9].

Weedy rice has become one of the most problematic worldwide rice weeds, and it belongs to the same species as cultivated rice, *Oryza sativa* L., which makes it morphologically similar to, and difficult to distinguish from, cultivated rice [10,11]. Weedy rice populations frequently have a red pericarp, thus explaining the "red rice" [12,13]. This weed has become particularly problematic throughout the world as a result of the diminished availability of low-cost labor and consequent increases in direct seeded rice [11,14]. Different techniques have been proposed to control this weed, but its management is still complex as a consequence of its similarity with cultivated rice and its biological variability [1,8]. For this reason, even though the introduction of rice varieties that are tolerant to herbicides has helped to control this weed, weedy rice can still cause severe rice yield losses [15,16]. Moreover, the red grains of weedy rice reduce the market value of rice because of the necessary extra-milling, which often results in broken grains [17,18].

Some hypotheses have been put forward to explain the origin of weedy rice in different rice cultivation areas throughout the world, such as a de-domestication process from cultivated rice varieties, evolution from wild rice through exploitation of the cultivated environment and outcrossing between cultivated and wild rice that often resulted in viable hybrids with weedy traits [13,19].

The reason for the high diversity of weedy rice, which is confirmed by the presence of different populations, is still far from being completely understood, even though it may be linked to the different origin processes of the populations [15]. However, the fact that weedy rice populations from different parts of the world, even though originating from multiple independent events, still share some common morphological and physiological traits, such as a red pericarp, seed dormancy and seed shattering, still has to be clarified [19,20]. Recent studies have suggested hybridization between weedy rice and rice as the main source of diversity in the species, but outcrossing between different weedy rice populations has also been hypothesized as contributing to the variability of this weed [21,22]. Moreover, other driving forces of the diversity of weedy rice are mutation, genetic drift and gene flow [23]. These processes are known to have caused different weedy rice populations to often develop similar morphological and physiological traits to those of cultivated or wild rice, or somewhere in between, but with high genetic diversity [24]. Extensive variations in many plant and seed traits, such as panicle morphology, plant height, tillering, awnedness, seed hull color, seed size, seed shattering and phenology, are found in weedy rice populations throughout the world [25]. These morphological and physiological traits allow weedy rice to be able to cope with different abiotic stresses, thereby giving it a competitive advantage over the crop, and a higher adaptability to different cropping systems and to changing environmental conditions [25].

Knowledge on the ability of the most troublesome rice weeds to respond to variable abiotic stresses and to adapt to different environments may be important to evaluate whether this weed will increase its competitive ability and threaten even more rice productions in the future, especially in consideration of the changing climate scenario. Many studies on weedy rice have been carried out and review papers have been written because of the importance of this weed in all over the world; some papers have recently also studied the effects of climate change on weedy rice [26,27].

This review presents a two-step approach to describe the success of weedy rice in many environments due to its ability to cope and adapt to abiotic stresses. In first step, some of the peculiar morphological and physiological traits that may permit weedy rice to succeed in the case of adverse climatic conditions are analyzed; in the second step, the most recent findings related to weedy rice behavior, in response to some abiotic stresses, such as temperature variations, drought, salinity and CO_2 increase, are reviewed.

2. The Morphological Traits of Weedy Rice That Confer the Ability to Face Abiotic Stresses

A morphological diversity of weedy rice can be found among the populations that grow in different areas, or even in the same zone but during different cropping seasons; this was previously highlighted in a weedy rice survey conducted in Italy, in which 150 weedy rice populations were described for their different morphological traits (Table 1) [25,28,29]. The high phenotypic variation of weedy rice may play a role in environmental adaptation and in the response to abiotic stresses present in different environments [30,31].

Table 1. Weedy rice trait variability (range) between 150 weedy rice populations collected in Italy (modified from Fogliatto et al., 2012).

Weedy Rice Traits	Trait Range between Weedy Rice Populations
Awn presence	awnless, mucronate, awned
Awn color	straw, black, brown
Awn distribution (section of the panicle in which are present awned grains)	tip only; 1/4 upper only; upper half only; 3/4 total length; whole length
Awn length (mm)	1.3–52.6
Hull coloration	straw, black, brown
1000 seed weight (g)	22.8–41.3
Number of seeds per panicle	80.3–205.7
Whole seed length (mm)	6.7–9.8
Whole seed width (mm)	2.6–4.2
Dehulled seed length (mm)	5.0–9.2
Dehulled seed width (mm)	2.3–4.4
Germination level at harvest (%)	0–33.9
Germination level at 10 days after harvest (%)	0–48.2
Germination level at 30 days after harvest (%)	0–73.8
Plant height (excluding panicle) (cm)	54.6–97.5
Flag leaf attitude of blade	erect, semi-erect, horizontal, recurved
Flag leaf length (cm)	18.3–46.2
Anthocyanin coloration of auricles and nodes	green, purple
Panicle attitude in relation to stem	Upright, semi-upright, slightly-drooping, drooping
Panicle attitude of branches	Erect, semi-erect, spreading
Panicle length (cm)	16.6–25.0

Weedy rice populations often mimic the rice crop nearby, even though some traits allow them to be distinguished [29,32]. The main morphological traits that can help to distinguish weedy rice from cultivated rice are related to both the vegetative structures (culm, plant size and tillering) and reproductive ones (panicle, seed shape, pericarp and hull coloration, and awnedness) [33,34]. However, the distinguishing traits are often not evident until tillering, which makes its early identification difficult.

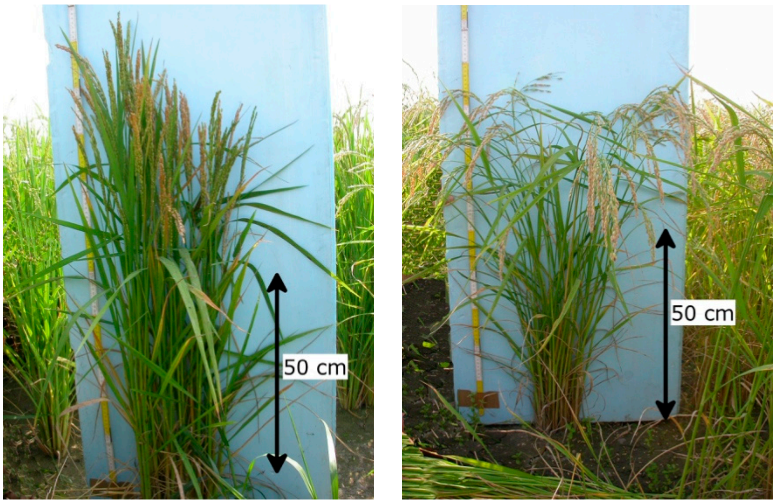
Some of these morphological distinguishing traits of weedy rice are directly correlated to the ability to face abiotic stresses; for example, plant height and canopy structure are two traits linked to light interception and the higher variability of weedy rice for these traits may help it to adapt to different environments [35]. Weedy rice high tillering is correlated with a more expanded root surface which in turn results in a higher nitrogen efficiency uptake, that can be advantageous in soil with limited resource supply [36].

Other morphological traits, such as seed morphology, hull color, awn presence and red pericarp, can indirectly help weedy rice to counter abiotic stresses, as they are often correlated with other advantageous physiological traits, such as seed dormancy and longevity [29].

Some of these traits will be analyzed in the following section.

2.1. Canopy Structure and Plant Height

Weedy rice has a canopy structure that varies from plant to plant; some populations have shown a less upright structure (sometimes sprawling), with an open canopy, than the tight and vertical canopy of rice (Figure 1) [11]. However, completely erect biotypes also exist; for example, some biotypes found in Mississippi rice fields in the 1980s were generally shorter and more erect than those previously found, mimicking the semi-dwarf rice cultivars introduced into the area at that time [13]. Some authors have suggested that a compact canopy structure of weedy rice can be an adaptive trait that allows the weed to be undetected in the field [13]. Moreover, it has also been found that a compact canopy still allows the weed to compete equally for light [27]. Moreover, as it has been proven that the competitive ability of rice is highly dependent on characteristics related to light interception [37], a higher competitiveness of weedy rice in different light environments is conceivable. The wide variability of the canopy architecture of different weedy rice populations can result in a better adjustment to variable environmental conditions.



(a) (b)

Figure 1. (**a**) A weedy rice population with a compact attitude and upright panicles (**b**) A weedy rice population with an open canopy and a spreading attitude of the branches and droopy panicles.

Weedy rice is usually 40% to 57% taller than cultivated rice [11]. A study conducted in Arkansas in the 2002–2004 period to characterize weedy rice populations noted that blackhull populations were taller and more variable than others. Sánchez-Olguín et al., [38] found the height of weedy rice increased faster than the height of rice crops. Weedy rice showed a biweekly height increase of 10–30 cm, as opposed to an 8–14 cm increase in cultivated rice for the same period. The plant height of Italian weedy rice was found to be similar in awned and awnless populations (about 80 cm), while it was lower in mucronate ones (very short seed awns) but, nevertheless, higher than that of cultivated rice [25].

Plant height is a characteristic that is generally thought to be influenced to a great extent by the growing conditions; nonetheless, plants that are genetically tall usually retain this trait across environments [29]. Taller plants have a competitive advantage over cultivated rice, because they can capture light more easily [36]. Moreover, taller plants with a more erect canopy structure can permit a higher penetration of light into the canopy, thus increasing the photosynthetic capacity of the plants [36]. Climate change may affect the overall availability of light during the rice growing season to a certain extent. For example, the current trends and predictions about the future climate in Italy (one of the areas at the northern rice cultivation limit) indicate the possibility of a precipitation reduction in spring and summer, mostly due to a decrease in the frequency of events [39]. This will likely result in less cloud and therefore an increased availability of light.

However, short weedy rice plants seem to have a field survival advantage when they have a similar height to that of cultivated rice, which allows them to be unrecognized (rather than to standout), and this can make it possible to control the weed by cutting the panicles with a cutting bar or by applying a broad-spectrum herbicide (e.g., glyphosate) using a rope wick bar applicator [40–42].

Plant height is regulated genetically by the *SD1* gene, which influences gibberellin biosynthesis; this in turn controls several growth traits, such as germination, tillering, flowering and height [43]. Semi-dwarf biotypes have been found to derive from a mutation of the *SD1* gene; this has resulted in a recessive allele, *sd1* (semi-dwarf 1), which is responsible for a reduction in plant height [43]. Shorter weedy rice plants do not have the advantage of being better at capturing light, but they are still highly competitive, as weedy rice is generally also more tolerant to shade [11]. The shade tolerance mechanism could be due to an increased chlorophyll b content, compared to chlorophyll a, which permits light to be harvested in a more efficient way under low light conditions [11]. A study conducted in the US found that weedy rice and rice grown under 50% shade conditions showed 46% and 38% reductions in photosynthesis, respectively [11]. Another study conducted on Asian weedy rice and cultivated rice also found that a shade of 50% was not able to significantly reduce the weedy rice seed production, even though they found high variability in shade tolerance between biotypes [44]. The higher tolerance to limited light availability could also represent an advantage for weedy rice in a scenario of reduced global radiation. The previous studies demonstrated a higher performance of weedy rice, even in the case of limited light availability.

2.2. Tillering

The tillering ability is usually higher in weedy rice than in cultivated rice. It is affected not only by the morphological characteristics of the plant, but also by intra- and inter-specific competition, rice seeding density and the height of the cultivated rice [28,29]. Plants with a high tillering ability can colonize an area faster and have a greater plant density and a higher competitive ability than those with a lower tillering ability [38]. An effective tillering, calculated as the ratio between the number of panicles and tillers per plant, shows the ability of plants to produce fertile tillers; this index has been found to be higher in weedy rice than in cultivated rice [45]. However, this trait only showed a limited variability within weedy rice biotypes and within cultivated varieties [45,46].

The higher tillering ability of weedy rice than of cultivated rice is related to a more efficient use of nitrogen and a greater capacity to direct nutrients toward shoot production [34]. Weedy rice can in fact produce more tillers and biomass per unit of uptaken nitrogen (N) than rice varieties [34,47]. Moreover, the high tiller production of weedy rice is correlated with its higher root surface and its greater ability to change its root architecture as a response to nutrient stress [48]. Fast weedy rice seedling growth is also linked to a more developed root system, with longer roots than rice [49]. Such a higher tillering ability and higher root surface allow weedy rice to be more competitive than rice, even in soils with a poor N content [36]. Soils with a low N content are expected to increase with climate change, as the variation in soil moisture and temperatures can affect nitrogen mineralization [50]; in these conditions, which will probably occur more often in developing countries [2], where the access to N fertilizers is more difficult, weedy rice problems will probably be further exacerbated.

2.3. Seed Morphology and Shape

Weedy rice seeds are usually shorter and wider than the cultivated varieties, except for short-grain cultivars [11]. However, a huge variability in seed shape can be observed among and even within biotypes [29]. Weedy rice populations throughout the world are generally classified as "medium grain", even though several biotypes are actually "long grain". Many of these "medium grain" populations in Italy range from 5.2 to 6.4 mm in length [28]. Fogliatto et al., [25] found that grains of awned populations can reach a length of 8 mm and are thus longer than those of awnless populations. The same study pointed out that mucronate and awnless populations have the narrowest and widest seeds, respectively. Studies conducted in the United States revealed that many biotypes have a grain length of about 8 mm, and that strawhull populations have shorter, thicker and wider grains than black and brownhulled groups [51].

Seed size has been shown to be correlated with seedling vigor, and larger seeds are thought to respond better to variable growing conditions and to survive hazardous stresses, such as drought and shade [49,52]. Some QTLs that control seed size have been found in the same regions as those coding for seedling traits, thus suggesting a close relationship between seedling vigor and seed size [49]. Moreover, as seedling growth depends on the reserves stored in the seeds, larger and heavier seeds are generally able to germinate better and can lead to more vigorous seedlings with a superior competitiveness [49,52]. In addition, seed weight can influence the ability of a seedling to emerge from a greater soil depth [53]. However, controversial results have been obtained for different species when correlating seed size and seedling growth [54]. As weedy rice populations have larger seeds than cultivated rice, they can have a faster initial seedling growth and greater ability to adapt to different environmental conditions [29,49]. A morphological study conducted on Italian weedy rice populations also found a high variability for this trait, with awned populations that were generally characterized by a higher seed weight, and mucronate populations (with very short awns) that were characterized by a lower seed weight [25]. However, it has been observed that even smaller seeds are able to produce more competitive seedlings than cultivated rice, thus suggesting that the higher competitiveness and adaptability of weedy rice is not exclusively linked to seed size or to a single trait [29,49]. This was also confirmed in the previously-mentioned study on Italian weedy rice populations, in which mucronate populations that had smaller and lighter seeds compensated for this disadvantage by showing a higher seed density per panicle and earlier panicle emission [25].

2.4. Hull Coloration and Awn Presence

Strawhull is the most dominant type of weedy rice in many rice growing areas throughout the world [33]. Blackhulls are less widespread, and brownhulls and grayhulls are minor groups [24]. Genetic studies using molecular markers have demonstrated that the phenotypic variability between strawhull and blackhull populations has a genetic basis [51,55–57]. Italian weedy rice populations are mainly of the strawhull type: more than 90% of the populations collected across the main rice growing areas in Italy were found to be strawhull, while the remaining 10% was equally composed of black and brownhull populations [25].

Awn length can vary from a few millimeters to as much as 10 cm; populations with very short awns are usually called "mucronate" (Figure 2) [29]. More than 95% of the strawhulls in the United States are awnless and about the same percentage of the blackhulls are awned [51]. Awn color can vary; strawhull populations mainly have straw-colored awns, but brown- and black-awned populations can also be found (Figure 2) [25]. Many populations have long and hispid awns that can adhere to the fur of domestic and wild animals and to human clothes, which helps their dispersal in different environments [11]. Awned populations are more competitive than awnless populations, and higher competitiveness has been demonstrated by blackhull populations than strawhull ones, together with a higher suppressive ability against other weeds [58]. Moreover, the greater morphological and physiological variability of awned populations than awnless ones can make them more adaptable to changing environmental conditions [25].

Hull coloration is linked to dormancy and the presence of awns, with awned blackhull populations generally showing a higher seed dormancy than awnless strawhull ones [29,59]. However, a great variation in the dormancy depth has been found for different weedy rice populations, even though a higher variability for this trait was found in blackhull biotypes [60]. Awned blackhull populations would probably have an advantage in the case of changing environmental conditions as they have a deeper seed dormancy that could permit the species to survive [34]. Moreover, it has been hypothesized that blackhull populations are better able to survive predation, as they cannot be detected by birds in the dark mud substrates of fields [13,57]. However, strawhull biotypes also have an advantage in paddy fields as they are similar to cultivated rice. The blackhull and brownhull types probably originated from hybridization between weedy/wild rice and cultivated rice; this outcrossing, which confers a great diversity, may result in a higher adaptability to variable growing conditions, and thus a greater weedy potential for blackhull and brownhull populations [11]. Moreover, it has been established that brownhull and blackhull grains resulted from the accumulation of pigments, such as flavonoids and anthocyanins [61]. Flavonoids have a role in protecting cells against damages due to ultraviolet light, in mediating germination signals and in the defense against pests [61,62]. Blackhull and brownhull weedy rice having higher contents of these pigments can have an advantage in high light environments.

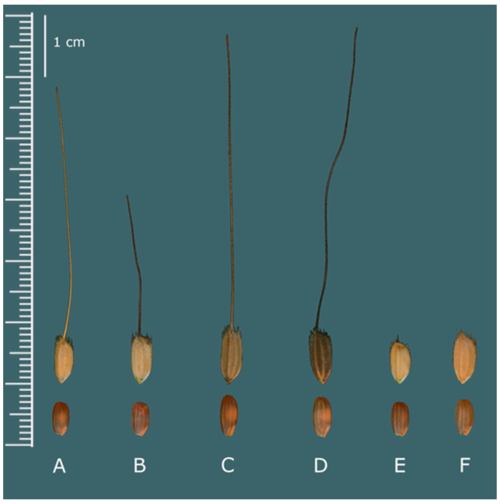


Figure 2. Examples of different Italian weedy rice populations with different hull and pericarp colors and variable presence, color and lengths of the awns. (**A**) straw-awned strawhull, (**B**) black-awned strawhull, (**C**) brown-awned brownhull, (**D**) blackawned blackhull, (**E**) mucronate strawhull, (**F**) awnless strawhull.

2.5. Red Pericarp

Weedy rice is also known as "red rice" because of the coloration of its pericarp, even though there are some populations that have white or light green pericarps [10,29,63]. The pigment that confers the red color to wild and weedy rice is proanthocyanidin, which is also called condensed tannin, and the *Rc* gene is a transcriptional regulator of proanthocyanidin synthesis [60,64]. A 14-base pair deletion on *Rc* gene confers the white color to rice, because this mutation produces a stop codon that results in a non-functionality of the transcription factor which inactivates the production of proanthocyanidin; the presence of this mutation is a marker of domestication [65,66]. Proanthocyanidins have been found to play a defense role against pathogens and predators, due to their deterrent effect [67], thus the presence of red pericarps in weedy rice can also contribute to its survival against pests [68].

Seed shattering, dormancy and *Rc* (red pericarp) QTLs (Quantitative trait loci) have all been found on chromosome 7. A linkage among these traits has been demonstrated, even though they exist in different regions of the chromosome [64]. Red pericarp has been favored in natural selection processes over white pericarp, as many weedy rice populations throughout the world have red pericarp; some studies have suggested that the production of proanthocyanidin is a weed-adaptive trait, which can also be suggested by the fact that the presence of red pericarp helps to control seed shattering and dormancy [65,69]. The maintenance of seed dormancy in the evolution of weedy rice has also promoted the selection of genotypes with other weedy traits, such as the presence of red pericarp and seed shattering, because of their linkage; the survival of these genotypes has in turn helped to maintain dormancy genes in weedy rice [70]. The absence of weedy traits, such as seed shattering, during rice domestication has indirectly led to select genotypes with a low level of seed dormancy [68]. Moreover, the mutation of *Rc* alleles, which has induced a white pericarp in cultivated rice, has also resulted in a reduction in dormancy [71].

Seed shattering and dormancy are thus weed-adaptive traits as they permit the conservation of the species in the seedbank and their persistence throughout several growing seasons by avoiding unfavorable environmental conditions [10,64,65,69].

3. The Physiological Traits of Weedy Rice That Confer the Ability to Face Abiotic Stresses

Weedy rice possesses some physiological traits that can be successful to counter adverse environmental conditions. A recent study found that weedy rice has about 18% of its genes related to abiotic stress and numerous adaptive traits that are not present in cultivated rice, such as high vigor and reproduction, that make it more tolerant to both abiotic and biotic stresses [31]. Moreover, weedy rice shows a high variability in relation to physiological traits, such as dormancy depth and flowering period, that can confer a high capacity to survive in stressful environments [31]. The presence of high diversity in genes that regulate plant growth, reproduction and stress tolerance help weedy rice to adapt and spread in different environments [72]. Below are presented some of the advantageous physiological traits of weedy rice.

3.1. Growth Vigor

The high growth, vigor and competitiveness of weedy rice are linked to the different previously mentioned morphological and physiological traits, such as taller plants, higher root area, greater plant biomass and high and protracted emergence [11]. High tillering in particular can help weedy rice to compete more by allowing it to occupy space quickly; the great leaf area and tallness permit a higher light interception than rice [11]. Moreover, it has been shown that weedy rice has a higher photosynthetic pigment content, chlorophyll a, b and carotenoids, than cultivated rice, and this has been correlated with a higher photosynthetic efficiency [49]. A higher efficiency of PSII electron transport, connected to a higher light absorption, due to a larger antenna size, and a greater energy transfer that leads to a higher net photosynthetic rate for weedy rice than for cultivated rice, have also been demonstrated [49].

A negative correlation between the photosynthesis rate and 1000 seed weight, seed size and early seedling emergence has been found, which means that plants originated from lighter seeds and early-emerged seedlings will not have a high photosynthetic efficiency [49]. Another study found a positive correlation between the weedy rice flag leaf length and plant height and the photosynthesis level; however, no significant differences in photosynthetic efficiency were found between weedy rice and cultivated rice [73].

3.2. Flowering and Ripening

It is known that weedy rice generally flowers earlier than cultivated rice [29]. In spite of this, a great variability exists among the different biotypes, and this variable flowering time increases its competitiveness in different environments [51,74]. The onset of flowering in a population depends on the length of the day (short photoperiods enhance rice flowering), the plant's age, the biotype and the latitude of its location [18]. The initiation time of flowering affects the ability of the plant to produce viable seeds, which ensures a high success of survival in any environment [74]. The florets of weedy rice open earlier in the day, usually between 08:00 and 09:00 a.m., and continue for at least one hour more than the cultivated varieties [18]. For this reason, and in spite of the fact that all rice species are basically self-pollinating, cross-pollination rates are higher in weedy rice than in cultivated varieties [18]. Pollen viability and longevity influence the level of cross-pollination; a study conducted in Australia found a similar pollen viability between weedy rice and rice, but the weed was ascertained to be able to produce more pollen grains and spikelets than cultivated rice [75].

Cases of cross pollination between weedy and cultivate rice have been documented extensively [10, 18]. The level of outcrossing between rice and the weed depends on some pre-zygotic barriers, such as differences in the flowering time, pollen viability, as well as in plant height, as pollen tends to fall to the ground and reach with difficulty the taller weedy rice plants [76]. Some studies have estimated that pollen only remains viable for a few minutes after being shed from the anthers, but such a time could be enough for cross-pollination [77]. Outcrossing can increase the genetic diversity of weedy rice and confer a survival advantage to the weed, as has occurred for the gene flow from herbicide resistant rice varieties [10,31,78]. Weedy rice and rice hybrids have been demonstrated to have a variable adaptability to different environments, with some plants showing heterosis for some competitive traits (i.e., plant height, spikelets per panicle), and other showing less advantageous characteristics (i.e., reduced shattering, low pollen viability), but in general no great difference in fitness has been observed between hybrids and weedy rice [10,79,80]. However, weedy and cultivated rice hybrids are usually vigorous, with a dominance of weedy traits, and it has also been demonstrated that the reproductive performance of such hybrids can increase over generations [10,79].

The heading date and dormancy in rice have shown both significantly positive and negative correlations in different studies, in which the QTLs for seed dormancy and for the heading date have been individuated in the same region of chromosomes 1, 3, 6 and 7 [81,82]. Two patterns of association between dormancy and flowering time have been found: some late flowering populations show a deeper dormancy than early flowering ones (a negative correlation between flowering time and seed dormancy), while other populations that flower earlier show a stronger seed dormancy than late flowering plants (a positive correlation between flowering time and seed dormancy) [82]. Even though the negative pattern in which late flowering populations have deeper dormancy than early flowering ones has been established to be the dominant behavior, both patterns contribute to the variability and to the success of weedy rice under different conditions [82]. Genotypes that flower later and have a deeper dormancy can better survive adverse environmental conditions and can ensure a higher seed bank persistence than early flowering less-dormant genotypes [82]. Early-flowering dormant genotype plants can have the advantage of mimicking the crop cycle and being undetected in the field, thereby avoiding harvesting [82].

Weedy rice populations reach maturity at slightly different times. Open panicle biotypes complete their life cycle 85–90 days post-emergence, while compact panicle types finish in 90–95 days [83]. According to another study, strawhull populations flower and mature at about the same time as cultivated varieties, but more quickly than blackhull populations (2 weeks earlier) [11]. On the other hand, another study, on southern US populations, found strawhull populations matured quicker than cultivated varieties, while blackhulls matured at a similar time to rice cultivars [51].

The synchronous flowering and maturation of weedy rice and rice can be beneficial for the weed, which has a greater chance of outcrossing with rice and of being accidentally harvested and re-planted with the crop seeds [27]. However, an earlier flowering can also be beneficial, as it allows the weed seeds to be stored in the seedbank, avoiding harvesting, thus guaranteeing their survival [74].

3.3. Seed Shattering

Seed shattering is a trait that is present in wild and weedy rice that facilitates their dispersal [27]. Shattering ability is determined by the formation of an abscission layer at the sterile lemma—pedicel juncture [83]. The cell layer never forms fully in cultivated rice; instead, bands of lignified tissue bind the spikelet to the pedicel [84]. There seems to be a relationship between seed shattering and other quantitative traits. Cai and Morishima [85] found several chromosomal regions where shattering QTLs and dormancy QTLs are linked. Gu et al., [86] found a significant correlation between awn presence, blackhull coloration and seed shattering.

The ability of weedy rice to spread and persist in fields has been attributed to shattering, as the seeds that are shed before harvest will probably be a part of the input of the seedbank; shattered seeds can remain dormant in the soil for many years avoiding unfavorable abiotic stresses, contributing to increase the species fitness in the environment (Figure 3) [30,87,88]. Moreover, shattering has been considered an adaptive trait, as seeds that persist on the plant can easily be predated by animals, and if seeds are non-dormant, they could germinate under unfavorable conditions [85]. Moreover, early seed shattering can prevent a loss of dormancy, which may occur after drying, and it has been established that a high moisture content confers a deeper seed dormancy [87].

(**a**) (**b**)

Figure 3. (**a**) Weedy rice panicles with several shattered seeds (**b**) Shattered weedy rice seeds lying on the soil surface.

3.4. Seed Dormancy and Longevity

The dormancy of weedy rice seeds is usually deeper and more persistent than that of cultivated rice, and this behavior is thought to be a strategy adopted to preserve the species in the case of unfavorable environmental conditions [89]. Different weedy rice populations display variable degrees of seed dormancy, probably due to the interaction of more than 10 QTLs that regulate seed dormancy in the weed; moreover, the interaction between genetics and environment is also responsible for the different degrees of dormancy of weedy rice [25,27,90]. Weedy rice dormancy is generally correlated with shattering, awn presence, blackhull biotype and seed pericarp color, traits that all together confer an advantage to the weed in agricultural environments [19,86,91].

Different environmental factors can affect weedy rice seed dormancy, and temperature is the key factor that controls dormancy removal [92]. It seems that temperature and its effect on dormancy is population-specific. A study of Italian strawhull awnless populations, stored at +5 °C, showed 20% of germination after about 20 days of storage, compared to a Louisiana strawhulled population in which dormancy was preserved and only broken after dehulling [93,94]. Germination in weedy rice is also enhanced by alternating temperatures; i.e., a daytime temperature fluctuating between 20 °C and 30 °C allows dormancy release [29]. The germination response to alternating temperatures has been proposed as a mechanism developed by plants to perceive canopy gaps in the crops or burial depths in soil, thereby contributing to the success of weeds in the environment [92]. Given the importance of temperature regimens in regulating seed dormancy and germination, a significant impact of climate change is foreseen for weedy rice germination patterns [95].

Dormancy depth is influenced by photoperiod sensitivity. Photo-insensitive species, such as rice, usually have a short dormancy period; dormancy in rice is related to maturity [29]. Light irradiation is not usually required by weedy rice or rice seeds to germinate; however, photoblastic seeds have been found among weedy rice varieties, and it has been demonstrated that these seeds are able to sense light proximal to the soil surface and germinate as a consequence [96]. This characteristic can further help weedy rice to succeed, as photoblastic seeds will only germinate under adequate light conditions, which also permit seedling development [96].

As already mentioned, besides having a primary or innate dormancy imposed by the mother plant upon seed release, weedy rice also displays secondary dormancy, that is, the ability to reenter into a dormant status as a response to changed environmental conditions; this mechanism can further protect weedy rice against unfavorable climatic variations [34]. Some studies have demonstrated that dormant weedy rice seeds are better able to resist high temperatures and humidity than non-dormant seeds [11] and this could help weedy rice survive under climate change.

A further weedy rice trait connected to dormancy is plant emergence, which can vary as a result of the differences in dormancy intensity between populations and it is generally more protracted in weedy rice than in cultivated rice [11]. Protracted and high emergences, together with rapid growth and biomass accumulation, permit weedy rice to develop more than cultivated rice and to better capture light and nutrients, thereby ensuring a good competitiveness and colonization capacity of the weed in different environments [38,49,97].

Seed longevity is linked to dormancy and the presence of red pericarp in weedy rice, but various studies have found contrasting results regarding its duration [29,98]. A US study found that more than 90% of weedy rice seeds were viable two years after burial; in another experiment, about 20% of the seeds were still able to germinate 7 years after burial [11,84]. In general, as deeper dormant seeds are viable for longer times, weedy rice is thought to have a higher longevity than cultivated rice [29]. On the other hand, cultivated rice, like all other crops, usually lacks most of the weedy/wild traits (seed dormancy, longevity, etc.) that allow weeds to tolerate unfavorable conditions, such as drought and salinity [89]. Longevity contributes to maintaining a high number of viable seeds in the soil seedbank, when the environmental conditions are not favorable for germination [98].

4. Weedy Rice Behavior under Abiotic Stresses Enhanced by Climate Change

Weedy rice, as pointed out in the previous sections, has a higher competitive ability and certain traits that help it to counteract the effects of changing environments and abiotic stresses [82].

The results of some studies related to weedy rice behavior, in the presence of particular abiotic stresses (temperature variations, drought, salinity and CO_2 increase), are reviewed in this section.

4.1. Temperature Variations

Higher temperatures will likely be common in the near future as temperature has been forecasted to rise by 1.8 to 4 °C by the end of the century [3]. It has been observed that the minimum daily temperatures are increasing more than the maximum daily temperatures [99]. Moreover, events of extreme temperatures, whether warm or cold, will also probably occur more often [100]. Rice and weedy rice, both of which have a C3 photosynthetic pathway, may be affected more by high temperatures than C4 species, especially during reproductive stage as high temperatures can affect biomass accumulation in this phase [101]. Even though C3 plants can have some potential benefits due to CO_2 increase, the adverse effects of elevated temperatures seem to be prevailing [101,102].

Confirmation of the disadvantage of C3 plants, compared to C4 ones, was demonstrated in a study conducted in Brazil in which weedy rice, rice and barnyardgrass were grown in a greenhouse at 25 °C and at 40 °C; the results showed that both weedy rice and rice showed a reduction in photosynthesis, gas exchange and protein content, compared to the C4 barnyardgrass [100].

A previous study that compared rice and weedy rice predicted that weedy rice will suffer less from rising temperatures than rice [99]. A mathematical model run to compare the growth behavior of Brazilian weedy rice and rice varieties under increasing temperatures found that the flag leaf of weedy rice emerged earlier than that of cultivated rice for temperature increases comprised between 3 °C and 5 °C, and this occurred in particular for late emergence dates and in strawhull populations rather than blackhull ones [99]. The faster growing cycle of weedy rice under high temperatures could imply an earlier heading and shattering time, which in turn would allow a faster increase in the soil seed bank prior to the rice harvest [99].

Low temperatures could also affect both rice and weedy rice, especially at the seedling stage or during flowering; it is likely that there will be an increase in the frequency of extreme events in temperate zones, as a result of climate change, including low temperature periods during these growth stages [29,103]. However, weedy rice has been shown to have several cold tolerance mechanisms, such as different antioxidant enzymes and gene expression in response to cold, which vary between *indica* and *japonica* weedy rice [103]. It was found that weedy rice collected in the USA, that experienced low temperatures during germination and early growth, showed higher seedling vigor and longer coleoptile and roots than cultivated rice at cold temperatures due to the presence of four QTL clusters on different chromosomes responsible for cold tolerance [104]. The high cold tolerance of weedy rice was further demonstrated by a study in which 133 weedy rice biotypes were evaluated on the basis of some physiological and genetical indicators; the study showed that about 40% of the accessions had a strong cold tolerance ability in terms of higher nitrogen recovery index, higher antioxidant enzyme content, such as SOD (super oxide dismutase) and MDA (malondialdehyde), and the expression of several genes related to cold tolerance [105]. Thus, several studies demonstrated that weedy rice can be a sources of cold tolerance genes for rice breeding [103–105]. Moreover, the temperature requirements for the germination of weedy rice in populations grown at high latitudes has been found to be lower than those grown at lower latitudes, thus demonstrating a great adaptability to germinate at different temperatures [106]. The viability of weedy rice seeds under low temperatures has been demonstrated to be higher than that of cultivated rice, especially in drier conditions, and this tolerance has mainly been related to the freezing resistance of the embryo and the activity of antioxidant enzymes that prevent seed deterioration [14,93,107].

4.2. Drought and Submergence

It has been forecasted that drought conditions, which are usually linked to increased temperatures, will be more severe as a consequence of climate change, and these two factors together can be the cause of stress and yield reductions in rice [2,7,27]. Drought can cause a reduction in the plant height, as a consequence of a photosynthesis decrease, in spike production and in seed weight, and in particular affects pistil development in the reproductive stage [7]. A recent study has predicted a possible occurrence of water scarcity for about 13 Mha of irrigated wetland rice in Asia by 2025 and that another 22 Mha of irrigated dry season rice will suffer economically from issues connected to water scarcity, such as limited availability of resources to access water [26]. As a response to these conditions, the adoption of direct dry seeded rice in Asia is gaining importance, as it requires less water than flooded seeding or transplanting [27,108]. A more widespread adoption of direct dry seeding will increase weed competition, especially for some species, such as weedy rice, whose growth is suppressed or limited by flooding water [27].

Again, in the case of drought, weeds can have a greater possibility of facing this stress, and weedy rice seems to have a better tolerance to drought than cultivated rice [10].

A study conducted in China on 61 weedy rice populations and coexisting rice cultivars collected in an equal number of sites and tested for germination under drought conditions found that weedy rice was much more tolerant to drought than cultivated rice in all the sites [108]. Moreover, the authors showed that *indica* weedy rice and *japonica* weedy rice populations were more tolerant to drought, in terms of germination, than their respective *indica* and *japonica* rice cultivars; *indica* weedy rice was also much more tolerant than the *japonica* rice varieties [108]. A possible explanation for the higher tolerance of weedy rice to drought, and to other abiotic stresses, compared to cultivated rice, is that the domestication process of the cultivars has led to a higher allocation of resources for reproduction than for traits that are useful to counteract abiotic stresses, as already demonstrated for weedy and cultivated sunflowers [109].

A recent study also found that some weedy rice accessions from China possessed specific proteins related to drought tolerance which resulted from the expression of some genes involved in the response to stresses [105].

Drought also seems to affect seed survival, as the storage of weedy rice under dry conditions can help to maintain seeds at a deeper dormant status, thereby prolonging their longevity [26,93].

Weedy rice can even tolerate drought in the reproductive phase, and it has been found that a short period of water stress of about 5 days at anthesis caused an increase in pollen production of about 10% in Malaysian weedy rice populations, while it caused a decrease in the same parameter of about 20% in cultivated rice [110]. Under the same conditions, the spikelet sterility percentage was also lowered in weedy rice, with maximum values of 23%, compared to cultivated rice, which showed maximum values of 50%, and this resulted in a higher seed production in weedy rice [110]. Another study found that pollen viability, after 10 days of drought before anthesis, was affected to a great extent in both weedy rice and rice, even though the pollen viability was slightly higher in the weedy rice, with reduction values of about 84% and 88% in weedy rice and rice, respectively. However, the slightly greater amount of pollen production in weedy rice still ensured a higher number of seeds than that of rice [75].

Photosynthesis is another parameter that is affected by drought, especially at anthesis, as demonstrated by a study in which the absence of water for 9 days prior to anthesis caused a reduction in the chlorophyll fluorescence parameters, which in turn led to a spikelet sterility of more than 80%, in both weedy rice and rice; however, the weedy rice populations showed higher fluorescence parameters than the cultivated rice, thus confirming a higher tolerance to drought conditions [111].

Submergence tolerance is another characteristic greatly variable in weedy rice, while in many cultivated varieties poor seedling establishment often occurs in case of heavy rainfall, poor drainage or in uneven field levelling [112]. The unfavorable submergence conditions may result in high yield losses in rice [112]. During flooding, seeds have to germinate in low aerobic conditions, which limit the respiration, creating an unsuitable environment for germination and seedling growth [113]. Deep flooding for short period after rice emergence is also one of the methods used to control weedy rice, for reducing its germination, emergence and growth [27,114]. However, the variability of weedy rice in flooding tolerance is great and some populations can be more tolerant to flooding than cultivated rice [114]. Specific genes regulating submergence tolerance in weedy rice can be used in breeding program to improve rice varieties [112,115].

4.3. Salinity

Water and soil salinity will be much more problematic in the near future due to climate change and both will be serious threats to rice cultivation [116,117]. Salinity is already affecting agriculture, as declared by UNEP (the United Nations Environment Programme), according to which about 20% of arable areas and 50% of crop land are already affected by salinity [9]. Soil salinization is mainly caused by a high evapotranspiration due to temperature increases, water overexploitation and salt water intrusion [118]. Rice is considered a relatively salt-sensitive crop, and sensitivity to salinity has been observed at germination, the early seedling stages and at reproduction [119]. Weeds also suffer from salinity conditions, but in general they are more tolerant to this stress than crops [26]. The same can be said for weedy rice, as previous studies demonstrated they have a better tolerance to salinity than cultivated rice; however, compared to other rice weeds, such as *Echinochloa* species, weedy rice is considered less tolerant [120,121]. The weedy rice germination was considered moderately affected by salty conditions in a study in which weedy rice showed 15% of germination up to 24 dS m^{-1} [122]. The same study also found higher shoot length at the same level of salinity in weedy rice than in other rice weeds [122]. Weedy rice often shows higher salinity tolerance than cultivated rice, as well as higher tolerance to other environmental stresses, as a result of the de-domestication process [123]. A study conducted on 74 weedy rice populations from China, together with cultivated rice varieties, detected a higher salt tolerance of weedy rice, in terms of germination and seedling growth, and this behavior was mainly attributed to the ability to regulate the Na^+/K^+ ratio in the plant, which permitted the detrimental effects of Na^+ ions to be limited; this ability of weedy rice was found to be due to the expression of several ion transport regulatory genes [123].

Different salt tolerance levels have been reported between herbicide resistant and sensitive weedy rice populations and rice varieties. A study conducted on a weedy rice population resistant to imazamox, an ALS inhibitor herbicide, and 4 sensitive populations, together with a Clearfield rice variety (tolerant to imazamox) and a conventional variety (Baldo), found that the germination of the herbicide resistant weedy rice and the tolerant rice variety were affected more by salinity than the herbicide sensitive populations and varieties [9]. However, this different behavior between the herbicide resistant weedy rice populations and the sensitive ones needs to be confirmed by further studies. Moreover, the presence of an association between herbicide resistance and salinity or other abiotic stresses is also worthy of investigation.

4.4. CO_2 Increase

Atmospheric CO_2 concentration have risen from about 284 μmol mol^{-1} in 1832 to values just above 400 μmol mol^{-1} in 2020, and the main cause has been attributed to the burning of fossil fuels, deforestation and the high food demand [3,124,125]. Some studies conducted in growth chambers predicted higher yields as a consequence of rises in CO_2; however, the results could be different in real field conditions and the CO_2 rise could have less impact than expected [3]. It has been estimated that the CO_2 level will increase by as much as 57% by 2050, or even more, reaching concentrations of 600–800 ppm, according to different predictive models [26]. C3 plants are probably those that will benefit the most from increasing CO_2 levels, while C4 plants will probably not be affected, as they already have biochemical pathways to concentrate CO_2 at the carboxylation site [26]. A yield increase of about 12% to 22% of the current production has been predicted for rice at higher CO_2 concentrations in temperate areas [126]. The available information suggests that, compared to the growth of C3 species, weeds will be more advantaged by the increase in CO_2 concentration than crops; this is likely to significantly alter the current competition interactions and may eventually result in an increase in yield losses [3,26].

The growth of weedy rice and its competitive ability will probably be enhanced by increasing CO_2 levels, as demonstrated in a study in which weedy rice showed a higher seed production and biomass for an increased CO_2 level (500 μmol mol^{-1}) than cultivated rice, and this behavior occurred in particular when weedy rice was planted at a high density (16 plants m^{-2} compared to a low density of 8 plants m^{-2}) [125]. Another study also found that weedy rice had an increased plant height, as well as an increased number of tillers and panicles for an elevated CO_2 level (600 μmol mol^{-1}), compared to cultivated rice; moreover, the increased CO_2 concentrations also caused a synchronization of the flowering time between weedy rice and a Clearfield rice variety, which enhanced the outcrossing rate, in particular from weedy rice to cultivated rice, thereby creating some hybrids that maintained herbicide resistance but also some undesirable weedy characteristics, such as seed shattering [127]. An interaction between increased CO_2 concentrations and high temperatures has also been found in another study in which weedy rice showed a greater biomass and seed production for all the tested increased CO_2 and temperature levels than cultivated rice [128].

5. Implications for Weedy Rice Control

This review has highlighted the possibility of a rise in the spread and competitiveness of weedy rice in rice fields due to the greater ability of the weed to respond to abiotic stresses enhanced by climate change. This could have implications on the control of weedy rice, and it underlines the necessity of integrating different control techniques. Preventive techniques, such as the use of certified seeds free from weedy rice, the use of clean machinery, early detection and the mapping of the presence of weedy rice, as well as agronomic techniques, such as the adoption of a stale seed bed, crop rotation, adequate fertilization and water management, are of fundamental importance [27,29].

A possible rise in the use of herbicides can be predicted in the case of strong weedy rice infestations, and the adoption of herbicide tolerant rice varieties will also probably increase. Clearfield rice varieties (tolerant to ALS-inhibitor imidazolinone herbicides) and Provisia varieties (tolerant to some ACCase inhibitor herbicides) have changed the control of weedy rice in the last few years, and their cultivation has risen since they were first adopted [129]. The risk of outcrossing between weedy rice and these herbicide tolerant varieties will also likely increase and some environmental changes, such as CO_2 increases, will further exacerbate this phenomenon [127]. Thus, farmers should be more rigorous in following the recommendations on the use of these technologies, such as that of avoiding the cultivation of tolerant varieties of the same technology (i.e., Clearfield or Provisia) for consecutive years in the same field [129,130].

Variations in the performance of herbicides should also be considered as a result of climate change, as environmental factors might reduce the suitable application time and may also affect the herbicide retention time on the leaf and its penetration, as the leaf surfaces may be thicker and more pubescent, with fewer stomata and more waxes [131]. Environmental changes may also affect the translocation and efficacy of herbicides. For example, temperature increases may raise the translocation of foliar herbicides, but may also cause their rapid metabolism, thereby reducing the efficacy of a treatment [131]. Moreover, the rise in CO_2 concentrations and temperatures may stimulate a higher root and shoot production in weeds, in some cases increasing the root/shoot ratio, which may lead to a dilution of the applied herbicides [131]. Changes in temperatures and CO_2 concentrations may indirectly reduce the efficacy of herbicides that act by inhibiting the activity of specific enzymes (such as the ALS-inhibitor herbicides), by lowering the quantity of proteins in plants, which would result in a lower demand of branched chain aminoacids [132]. Some studies that were conducted to evaluate the changes in herbicide efficacy due to climatic variations suggested that the influence of environmental factors can vary not only among herbicides with different modes of action but also between herbicides with the same mode of action, therefore making generalization very difficult [132]. Thus, it is important to consider that the herbicide physiology in plant can be modified as a consequence of environmental changes [131,132].

Rice transplanting is still common in many rice cultivation areas in the world. However, the shift from this technique to direct seeding is increasing and this trend will probably continue as water availability progressively reduces [16]. Even though direct seeding has a number of advantages, such as water and labor saving and better rice establishment, weedy rice will probably be more problematic, and weed control in general could be more difficult because of the simultaneous emergence of weedy rice and rice, which may reduce the quantity and quality of rice yield and possibly increase rice production cost at the same time [16,27].

Considering the forecasted future increased occurrence of environmental changes, the use of abiotic stress tolerant rice varieties will be particularly important [26]. Testing the rice varieties currently available for their tolerance to abiotic stresses will be crucial as will the development of new abiotic stress tolerant varieties. For example, recent studies have discovered that the Baldo rice variety is relatively saline tolerant. This variety is one of the most frequently cultivated rice varieties in Italy and in other rice areas, it is also important for the export market, and it has shown a higher tolerance to salt than the traditional Vialone Nano variety [9,133]. Moreover, the discovery of different biotic and abiotic stress tolerance genes in weedy rice could be useful in breeding programmes to improve the response of rice to climate changes [10]. The higher seed production of weedy rice at elevated temperatures, together with its higher tolerance to salinity, drought, elevated CO_2 concentrations and cold are important traits that could be analyzed for specific genes that control these behaviors and then used to develop new rice varieties with these characteristics.

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