# Shattercane (*Sorghum bicolor* (L.) Moench Subsp. *Drummondii*) and Weedy Sunflower (*Helianthus annuus* L.)—Crop Wild Relatives (CWRs) as Weeds in Agriculture

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Abstract: Shattercane (*Sorghum bicolor* (L.) Moench subsp. *drummondii*) and weedy sunflower (*Helianthus annuus* L.) are two examples of crop wild relatives (CWRs) that have become troublesome weeds in agriculture. Shattercane is a race belonging to a different subspecies than domesticated sorghum (*Sorghum bicolor* (L.) Moench subsp. *bicolor*). Weedy sunflower populations are natural hybrids between wild and domesticated sunflower (*Helianthus annuus* L.). Both species have key weedy characteristics, such as early seed shattering and seed dormancy, which play an important role in their success as agricultural weeds. They are widely reported as important agricultural weeds in the United States and have invaded various agricultural areas in Europe. Shattercane is very competitive to sorghum, maize (*Zea mays* L.), and soybean (*Glycine max* (L.) Merr.). Weedy sunflower causes severe yield losses in sunflower, maize, soybean, pulse crops, and industrial crops. Herbicide resistance was confirmed in populations of both species. The simultaneous presence of crops and their wild relatives in the field leads to crop–wild gene flow. Hybrids are fertile and competitive. Hybridization between herbicide-tolerant crops and wild populations creates herbicide-resistant hybrid populations. Crop rotation, false seedbed, cover crops, and competitive crop genotypes can suppress shattercane and weedy sunflower. Preventative measures are essential to avoid their spread on new agricultural lands. The development of effective weed management strategies is also essential to prevent hybridization between sorghum, sunflower, and their wild relatives and to mitigate its consequences.

Keywords: seed shattering; yield loss; herbicide resistance; hybrid fitness; weed management; preventative measures; cultural practices

1. Introduction

Crop wild relatives (CWRs) are wild plant species closely related to domesticated crops. According to Maxted et al. [1], the genetic relationships between crops and CWRs are described by the following taxa groups: TG1a—crop taxon; TG1b—the same species of crop; TG2—the same series or section of crop; TG3—the same subgenus of crop; TG4—the same genus of crop; and TG5—the same tribe, but different genus of crop. The species in taxa groups TG1a, TG1b, TG2, and TG3 are of unique interest from both plant breeding and weed science perspectives because they belong in the primary gene pool of a genus (GP–1) and can successfully interbreed [2–5].

These wild taxa are valuable genetic resources that should be explored for use in plant breeding programs. They can increase genetic diversity in cultivated species through

hybridization and they can transfer beneficial traits such as resistance to biotic and abiotic stress factors. CWRs were successfully used to confer resistance traits to soil salinity, drought, and bacterial leaf blight in durum wheat (*Triticum durum* Desf.), barley (*Hordeum vulgare* L.), and rice (*Oryza sativa* L.), respectively [6–8]. Adaptation of crops to stress conditions through the use of CWRs leads to improved crop yields, yield stability over time, and the improved quality of agricultural products. For example, in soybean (*Glycine max* (L.) Merr.), a wild relative of the crop was reported to have candidate genes that improve 1000-seed weight and thus soybean seed yield [9]. In processing tomato (*Solanum lycopersicum* L.), CWRs belonging to the same genus contain genes that can improve fruit quality traits, such as total soluble solids content, sugar content, and the fruit dry weight to fruit fresh weight ratio [10]. Similar results were reported for cereals and legumes [11]. The use of CWRs is also recommended for crop improvement in dominant multipurpose crops such as sorghum (*Sorghum bicolor* (L.) Moench subsp. *bicolor*) and sunflower (*Helianthus annuus* L.) [2,12].

However, wild species that are closely related to domesticated crops can occur as weeds on agricultural lands. A special group of agricultural weeds includes weedy relatives of some crops that belong to the same species as domesticated plants. In particular, weedy rice (*Oryza sativa* L.), shattercane (*Sorghum bicolor* (L.) Moench subsp. *drummondii*), and weedy sunflower (*Helianthus annuus* L.) are prominent examples of weedy relatives of rice, sorghum, and sunflower, respectively [13–15]. All these species are competitive and have undesirable agronomic characteristics, such as early seed shattering and seed dormancy, which play an important role in their success as weeds in agriculture [15–17]. Although the seeds can be assumed to be edible, they cannot be harvested because seed shattering occurs before crop maturity [14,18,19]. In addition, seed dormancy allows these wild plants to form large seed banks in the soil and become persistent in agricultural areas [15,20,21].

Shattercane and weedy sunflower are among the most competitive weeds against their closely related domesticated crop species, namely sorghum and sunflower, respectively [22,23]. Furthermore, both are troublesome species in a variety of crops. In particular, shattercane was reported to cause significant yield losses in maize (*Zea mays* L.) and soybean (*Glycine max* (L.) Merr.); weedy sunflower competition was reported to limit the productivity of maize, soybean, pulse crops, and industrial crops [24–28]. On the contrary, weedy rice exclusively infests rice fields and causes severe yield losses everywhere in the world where direct-seeded rice is cultivated [15,19]. Apart from their competitive ability, populations of these weedy crop relatives have developed resistance to common herbicides used to control weeds in summer field crops [29]. In addition, strong genetic and botanical ties favor hybridization between weedy and cultivated plants, leading to more complex weed problems. It should be noted that wild plants contribute to crop improvement when gene flow occurs from CWRs to domesticated plants, under controlled conditions. On the other hand, if there is natural gene flow from the crop to its wild relatives in the field, this leads to the development of fertile hybrid populations that have comparable fitness to their wild and domesticated parents [3,4]. In cases where the domesticated parent is a herbicide-tolerant crop, the crop–weed gene flow can lead to the development of herbicide-resistant hybrid populations [30,31].

Gene flow from crops to their wild relatives occurs by cross-pollination [32]. The pollen parents of the first outcrossing may be domesticated plants in cultivation, crop volunteers that arose after the harvest of the previous crop, or feral populations that escaped cultivation. The terms 'crop volunteers' and 'feral populations' are explained in later sections, as is the crucial role of such plant populations as genetic bridges for the success of the crop–weed gene flow under certain circumstances [3,33,34]. In outcrosses of sorghum × shattercane and rice × weedy rice, pollen is transferred by wind from the crop plants to their wild relatives [35–37]. In contrast, cross-pollination between domesticated and wild forms of *H. annuus* occurs by insects, especially honeybees (*Apis mellifera* L.), since *H. annuus* is an insect-pollinated species [38,39]. The hybridization process begins when desiccated pollen grains (from the flowers of the domesticated plants) land on the

stigma (in the flowers of the crop's wild relatives). The male gametophytes (e.g., pollen grains) rapidly rehydrate and begin to germinate [40]. Subsequently, a pollen tube grows through the pistil tissues of the stigma and style, across the surface of the placenta, and then through the micropyle of the ovule to reach the female gametophyte in the embryo sac [40,41]. The growth of the pollen tube stops, and two gametes are released [40]. It should be noted that pollen tube growth is both polar and directional. Cytosolic Ca^{2+} ions are thought to play an important role in pollen tube formation, growth, and polarity as secondary messengers [40,42,43]. In any case, the physical distance between crop plants and their wild relatives and the synchrony of their flowering times are crucial factors affecting hybridization rates [18,37].

The current study summarizes information on weedy relatives of crops that are problematic weeds in agriculture because they compete with a wide range of crops, have high invasive potential, and can also successfully interbreed with their closely related domesticated crops and generate complex weed problems [32]. Regarding species selection, it should be noted that shattercane and weedy sunflower are problematic species in a wider range of crops compared to weedy rice. Moreover, the interactions between weedy rice and rice and the appropriate strategies to control weedy rice in direct-seeded rice fields were recently studied [15,19]. Therefore, the present study focused on the weedy relatives of sorghum and sunflower, i.e., shattercane and weedy sunflower, respectively. Although the selected species are known to be important weeds mainly in the United States, there is much evidence that they have also invaded various agricultural areas in Europe [44,45].

First, we present information on the origin of these species and also on their important morphological and ecological traits. Then, we summarize information on their competitive ability against their closely related domesticated species and also against other important summer field crops. In addition, we include information about their occurrence in Europe where they have the potential to become serious invaders in the future. Cases are presented where herbicide resistance was confirmed. Evidence of successful hybridization between crops and their wild relatives is included along with information on the fitness of the hybrids produced; we also include cases where crop–wild gene flow led to the development of herbicide-resistant hybrids. Weed management strategies that can be effective in controlling these species are discussed. Emphasis is also placed on the role of weed management in preventing gene flow from crops to their wild relatives.

2. Shattercane [*Sorghum bicolor* (L.) Moench Subsp. *drummondii*]

2.1. Origin

The genus *Sorghum* is divided in five subgenera, namely *Eu–sorghum*, *Chaetosorghum*, *Heterosorghum*, *Parasorghum* and *Stiposorghum*. The *Eu–sorghum* subgenus includes the following species: *Sorghum bicolor* (L.) Moench, *Sorghum propinquum* (Kunth) Hitchc., *Sorghum halepense* (L.) Pers., and *Sorghum almum* Parodi [46].

Sorghum bicolor (L.) Moench is divided into three subspecies whose members are all diploids (2n = 20): (1) *Sorghum bicolor* (L.) Moench subsp. *bicolor* which contains all cultivated sorghum lines classified by Harlan and De Wet [47] into five races (*bicolor*, *guinea*, *caudatum*, *kafir*, and *durra*), (2) *Sorghum bicolor* (L.) Moench subsp. *verticilliflorum* (Steud.) de Wet ex Wiersema & J. Dahlb. which contains wild progenitors of cultivated sorghums classified into four races, namely *aethiopicum*, *arundinaceum*, *verticilliflorum*, and *virgatum* [48] and (3) *S. bicolor* ssp. *drummondii* (Nees ex Steud.) De Wet ex Davidse which includes two races called sudangrass and shattercane [48]. This subspecies is the product of natural hybridization between *S. bicolor* subsp. *bicolor* × *S. bicolor* subsp. *verticilliflorum* [46]. While sudangrass can be grown as a forage crop, shattercane is a weedy relative of sorghum that is a considered a serious weed whose agronomic importance has increased over the years [14,26,27,31,46,49–51].

As for the other species of the *Eu–sorghum* subgenera, *S. propinquum* is a diploid (2n = 20), rhizomatous, biennial to perennial, wild species [52]. *S. halepense* is another rhizomatous perennial wild species, which is tetraploid (2n = 40), also known as john-

songrass [52]. This species is thought to have arisen either by natural hybridization between *S. bicolor* × *S. propinquum* or by chromosome duplication in *S. propinquum* [14,53]. Regarding *S. almum*, it is a tetraploid (2n = 40), rhizomatous, perennial species and is a natural hybrid between *S. bicolor* × *S. halepense* [54]. Of the perennial species presented, *S. propinquum* and *S. almum* are not reported as troublesome weeds [16]. In contrast, johnsongrass is one of the most common and noxious weeds in agriculture, which can also reduce biodiversity due to its high invasive potential [55].

This article could focus on both shattercane and johnsongrass, as both species are troublesome weeds that can hybridize with the crop [2,3]. However, the present study focuses on species that belong to the primary gene pool (GP–1) of a genus and have very strong genetic links to the crop. Species in this primary gene pool readily interbreed and produce fertile hybrids [16]. In contrast, species belonging to the secondary gene pool (GP–2) of a genus can also interbreed with the crop, but successful gene transfer between these two gene pools can be difficult in some situations. Since shattercane belongs to the primary gene pool (GP–1) of sorghum while johnsongrass belongs to the secondary gene pool (GP–2) of the genus [2], further information is provided only on shattercane. In addition, the main aspects of johnsongrass biology and ecology, as well as its negative impacts on agriculture and biodiversity, were already summarized in a previous study [5].

2.2. Morphological and Ecological Traits

Shattercane is a warm-season annual grass that originated in Africa [46]. The plants have erect, unbranched stems and can grow 1–4 m tall. This weedy race has some key characteristics that explain its evolution into a troublesome weed. First of all, plant height cannot be regulated in shattercane because it lacks a dwarfing trait that is controlled in cultivated sorghum by four recessive dwarfing genes [56]. Therefore, the increased canopy height results in lower harvest index values and makes mechanical harvesting an impossible task [21]. It should also be noted that the great height of shattercane improves its ability to compete with tall cereals such as maize (*Zea mays* L.) and increases its ability to disperse seeds over long distances [57].

As for seed dispersal, it is an ecological trait playing a central role in the success of this species as an agricultural weed. Seed dispersal is rapid, and the explanation lies in the abscission layer that forms at the base of the spikelet at the stage of physiological seed maturity. This abscission layer allows the seed to detach from the panicle and immediately fall to the soil surface. It is worth mentioning that only a light breeze (e.g., a wind moving at a very low speed of 7–12 km h^{-1}) is adequate to cause seed shattering before the cultivated crop can be harvested [14]. In addition, the shattered seeds can stay dormant for a long time in the soil and remain viable. Burnside et al. [58] reported a seed survival period of up to 13 years in the United States while Fellows and Roeth [59] found that the dormancy period can be further extended if the seeds are tightly enclosed in the glumes. As for the reproductive ability of shattercane, plants typically produce 1–6 panicles with each panicle producing 500–1500 seeds [57]. An interesting fact is that shattercane has an extended emergence window since the seeds can germinate late in the growing season. These later-emerging weeds may exhibit aggressive growth rates, reach maturity, and produce seeds that enrich the species' seedbank dynamics in the soil [14].

2.3. Competitive Ability and Distribution

Shattercane populations can establish on agricultural land, field margins, and marginal areas in various regions across the world. Its presence as a weed was reported in North America, in Africa where it is believed to have originated, in Asia, and also in Europe [16,27,44,46,49,60]. Shattercane infestations result in significant yield loss in important summer field crops including grain sorghum, maize, and soybean. All reports of yield loss due to shattercane competition are from field trials conducted in the United States, with the exception of the case study by Raey et al. [27], which was conducted in Iran, Asia (Table 1).

Table 1. Yield losses of summer field crops due to shattercane (*Sorghum bicolor* (L.) Moench subsp. *drummondii*) interference. Results presented are from field trials repeated in time or space.

Crop	Shattercane Density	Yield Loss	Reference
Grain Sorghum	5.6 Plants m^{-2}	73–82%	[61]
Maize	13–20 Plants m^{-1} of Row	22%	[49]
Maize	20 Plants m^{-2}	43–85%	[51]
Maize	6.6 Plants m^{-2}	19%	[26]
Maize	40 Plants m^{-2}	34%	[62]
Soybean	3.3 Plants m^{-1} of Row	60%	[63]
Soybean	12 Plants m^{-2}	57%	[27]

Especially in the United States, shattercane is one of the most common and problematic weeds in grain sorghum [50]. There are also case studies from this continent showing the competitive ability of shattercane against domesticated sorghum and other important summer field crops. In sorghum, early studies revealed that 5.6 shattercane plants m^{-2}, spaced 45 cm apart, caused a 73–82% yield loss in grain sorghum [61]. The competitive advantage of shattercane compared to grain sorghum growth was also recently highlighted in greenhouse studies [21,31,36,64,65]. In most of the case studies mentioned, shattercane exhibited a more aggressive growth compared to grain sorghum and the weeds were significantly taller than the domesticated plants. Shattercane is also reported as a strong competitor to maize and soybean. In particular, Beckett and Stoller [49] found that 13 to 20 shattercane plants m^{-1} of row resulted in a 22% grain yield loss in maize. Season-long shattercane interference (from 20 plants m^{-2}) reduced grain yield by 43–85% in the study by Hans and Johnson [51]. The same authors also observed significant yield reductions when shattercane was left uncontrolled until it was 31 cm tall. At a density of 6.6 plants m^{-2}, Deines et al. [26] predicted a grain yield loss of 19%. King and Hagood [64] found that shattercane competition (at a density of 40 plants m^{-2}) resulted in up to 34% grain yield loss. In soybean (*Glycine max* (L.) Merr.), seed yield decreased by more than 60% due to full-season competition by 3.3 shattercane plants m^{-1} of the row [65]. There is also evidence from Asia showing that 50 soybean plants m^{-2} were outcompeted by 12 shattercane plants m^{-2} and suffered a 57% loss in seed yield [27].

There are not many official reports on the presence of shattercane in Europe. However, it should be noted that in the context of climate change, the resilient and versatile sorghum has gained importance as a multipurpose crop in Europe [66]. Sorghum acreage has increased in all European sorghum producing countries, namely France, Italy, Hungary, Romania, Bulgaria, Austria and Greece [67]. Defelice [14] pointed out that shattercane can spread anywhere in the world where domesticated sorghum is grown. Therefore, it is possible that populations of shattercane have developed in the European countries mentioned above, although this is not officially reported. The U.S. Department of Agriculture (USDA) has conducted a weed risk assessment for this weed species and concluded that the presence of shattercane in sorghum producing countries is underreported because it is difficult to distinguish shattercane from sorghum [68]. Berenji and Dahlberg [44], Dahlberg et al. [69] and Schwartz–Lazaro and Gage [70] mention that there are at least two distinct areas where shattercane populations were reported, namely southeastern Hungary and northeastern Serbia. Dahlberg et al. [69] also included a photograph of a shattercane population growing in a broom corn field in their study. Broomcorn is a cultivated race of sorghum whose panicles are used as raw material for making natural corn brooms [71]. The morphology of shattercane is very similar to broom corn. Since Europe, especially Hungary, Romania and Serbia, are the main producers of broom and broom corn in the world [44], it is logical to assume that populations of broom corn may have developed in these areas but are not yet reported due to the morphological similarities between broom corn and shattercane. In view of this situation, a research goal of weed scientists in Europe should be to carefully survey sorghum fields to detect populations of shattercane and take action to control this weed before it becomes established in Europe.

2.4. Herbicide Resistance

Research has shown that consecutive applications of ALS (acetolactate synthase)-inhibiting herbicides in a particular field inevitably result in the selection of ALS-resistant shattercane populations (Table 2).

Table 2. Cases of herbicide resistance in shattercane (*Sorghum bicolor* (L.) Moench subsp. *drummondii*) populations. Results presented are from temporally and spatially replicated dose-response experiments.

Crop	Herbicide	Mode of Action	Chemical Family	Reference
Maize	Primisulfuron–Methyl	ALS Inhibitor	Sulfonylurea	[72]
Maize	Primisulfuron–Methyl Nicosulfuron Imazethapyr	ALS Inhibitor ALS Inhibitor ALS Inhibitor	Sulfonylurea Sulfonylurea Imidazolinone	[73]
Maize–Soybean Rotation	Primisulfuron–Methyl Nicosulfuron Imazethapyr	ALS Inhibitor ALS Inhibitor ALS Inhibitor	Sulfonylurea Sulfonylurea Imidazolinone	[74]
Maize	Imazethapyr	ALS Inhibitor	Imidazolinone	[75]
Maize	Nicosulfuron Imazethapyr Imazapyr	ALS Inhibitor ALS Inhibitor ALS Inhibitor	Sulfonylurea Imidazolinone Imidazolinone	[64]
Maize–Soybean Rotation	Nicosulfuron Imazethapyr	ALS Inhibitor ALS Inhibitor	Sulfonylurea Imidazolinone	[76]

Anderson et al. [72] reported shattercane resistance to primisulfuron–methyl in a biotype collected from a maize field treated with primisulfuron–methyl and nicosulfuron for three consecutive growing seasons. In the study by Lee et al. [73], shattercane populations from 12 fields were resistant to primisulfuron–methyl and nicosulfuron. In the same study, another population was susceptible to primisulfuron–methyl and nicosulfuron but resistant to imazethapyr. The presence of a biotype with noticeable levels of resistance to primisulfuron and cross-resistance to nicosulfuron and imazethapyr was also confirmed [74]. Resistance evolved after 10 years of use of ALS–inhibiting herbicides in a field where maize was rotated with soybean. Zelaya and Owen [75] observed that one population was 29 times more resistant to imazethapyr compared to a sensitive population. These authors noted that resistance occurred in an environment where the use of ALS-inhibiting herbicides was an important component of the selection pressure. In another study, the continuous use of nicosulfuron for weed control in silage maize resulted in the selection of a shattercane population that was resistant to nicosulfuron and exhibited cross-resistance to imazethapyr and imazapyr [64]. Werle et al. [76] screened 190 shattercane populations and observed five and four populations that were resistant to imazethapyr and nicosulfuron, respectively, and two populations that were cross-resistant to nicosulfuron and imazethapyr. All of these cases of herbicide resistance in shattercane were reported in the United States. However, if shattercane becomes a serious invader in European fields, crop rotation and herbicide rotation practices should be used to prevent the development of herbicide-resistant populations.

2.5. Hybridization with Domesticated Sorghum

Both shattercane and sorghum belong to the primary gene pool of the genus, they are sexually compatible, and can be wind pollinated. Therefore, these sympatric species can successfully outcross under favorable field conditions and produce fertile hybrids [21,36,60]. Schmidt et al. [37] highlighted flowering duration of sorghum and flowering overlap between the two species as important factors determining hybridization rates in the field. The same authors also emphasized the crucial role of wind speed and

direction in the outcome of the hybridization process [37]. Moreover, hybridization rates tend to increase when the distance between interacting populations becomes smaller [3,37]. Another noteworthy point is that gene transfer from the crop to its wild relatives is more frequent than gene transfer in the opposite direction [77]. One possible explanation is that populations of domesticated plants in agricultural fields are usually much larger, and the domesticated plants, therefore, produce larger amounts of pollen compared to their wild relatives [77].

In any case, hybrids between sorghum and shattercane can be competitive, as shown by case studies where successful hybridization was reported. Sahoo et al. [36] found that grain sorghum × shattercane hybrids produced 31% more biomass and were 56–61% taller compared to grain sorghum. They also found that the hybrids produced 40–63% and 42–61% more spikelets per panicle and seeds per plant, respectively, compared to their domesticated parents. In this study, hybrid relative fitness was similar to shattercane as also observed in the study by Schmidt et al. [37]. In the study by Magomere et al. [78], F_1 hybrids produced 1509 more seeds than their parent plants, while the mean seed weight of the hybrids was 41% higher than that of grain sorghum. Similar observations were made for aboveground biomass production and tillering capacity, indicating a competitive advantage of the F_1 hybrids over their domesticated parents [78]. Schmidt et al. [21] revealed also that F_2 hybrids are characterized by lower vegetative growth and fecundity than shattercane but their relative fitness can be comparable to that of grain sorghum. In particular, these authors reported no significant differences between grain sorghum and grain sorghum × shattercane F_2 hybrids in the number of panicles per plant, aboveground biomass production, and seed production [21]. In the pot experiments by Werle et al. [31], F_1 hybrids outcompeted an ALS–resistant grain sorghum inbred line and caused a biomass yield loss of 75–95%. Aside from their competitive ability, seed dormancy is another characteristic of these hybrids that might enable them to be highly persistent on agricultural lands. Indeed, there is evidence that seed dormancy is similar to shattercane and seeds can survive in the soil for many years [3,21,36].

Another consequence of hybridization between domesticated sorghum and its wild relative, shattercane, is the emergence of herbicide-resistant hybrids under certain circumstances. First, it should be noted that in the past, germplasm from shattercane populations with resistance to ALS-inhibiting herbicides was used to develop the 'Inzen' technology, i.e., to develop ALS-tolerant grain sorghum populations [79]. Werle et al. [63] revealed that most of herbicide-resistant shattercane populations have evolved independently and resistance is not the result of pollen-mediated gene flow between ALS-tolerant grain sorghum and shattercane. However, there is evidence that possible outcrossing between the crop and its wild relative may indeed result in the creation of ALS-resistant grain sorghum × shattercane hybrids. For instance, Werle et al. [23] found that shattercane × ALS–tolerant grain sorghum hybrids were tolerant to ALS-inhibiting herbicides and herbicide application did not reduce hybrid growth. Adugna and Bekele [60] also reported that such hybrids can be tolerant to herbicides and at the same time competitive against grain sorghum and exhibit similar fitness to shattercane. In another study conducted under greenhouse and real field conditions, the creation of ALS-tolerant hybrids was confirmed as the hybrids were not affected by the application of a nicosulfuron plus rimsulfuron mixture and maintained their competitive advantage over their ALS-tolerant grain sorghum parents [31].

3. Weedy Sunflower (*Helianthus annuus* L.)

3.1. Origin

The genus *Helianthus* is native to the temperate zones of North America and includes 52 species and 19 subspecies with 14 annuals and 39 perennials. The basal chromosome number is n = 17. All 14 of the annual species are diploid (2n = 34), while in the group of perennial species there are 26 diploid, 3 tetraploid (2n = 68), 7 hexaploid (2n = 102) and 3 mixaploid species [80,81]. Taxonomically, there are four distinct sections in the genus, namely the annual polyphyletic section *Helianthus*, the annual monophyletic section

Agrestis, the perennial polyphyletic section *Ciliares* with two races, and the perennial polyphyletic section *Divaricati* with four races [82]. The species *Helianthus annuus* L. of the section *Helianthus* includes the domesticated sunflower (*Helianthus annuus* L. var. *macrocarpus*) cultivated for its oil seeds and also its weedy or wild forms [83].

In an early study by Heiser [84], it was suggested that there are three subspecies of *H. annuus*, namely *H. annuus* subsp. *lenticularis*, *H. annuus* subsp. *texanus*, and *H. annuus* subsp. *annuus*, the last subspecies being emphasized as the weedy sunflower. However, there are still no official names for the subspecies. In another study, Heiser [83] emphasized that *H. annuus* exhibits high morphological variability, so that its wild and weedy relatives cannot be adequately classified into separate subspecies. This is in contrast to the genus *S. bicolor*, where shattercane is a race belonging to a different subspecies than the domesticated sorghum. Indeed, there is strong evidence that the weedy forms of *H. annuus* are not represented by a specific subspecies but are the natural result of hybridization with domesticated sunflower. There is evidence of crop introgression in weedy sunflowers since they combine wild and domesticated traits in proportions that vary between wild and domesticated plants [4,85–88]. In some recent studies, the various forms of *H. annuus* are divided into the domesticated sunflower, the weedy sunflowers, which include the "agrestal" biotypes, and the wild sunflowers, which include the "ruderal" biotypes. The term "agrestal" is used to describe plants evolved under selection pressure on agricultural land while the term "ruderal" refers to plants inhabiting naturally disturbed sites [89].

For the species *H. annuus*, the weedy "agrestal" biotypes are considered natural crop–wild hybrids [4,13,20,22]. The initial invasions of such biotypes on agricultural land might be attributed to importations of contaminated sunflower seed lots. The importations of contaminated seed from the United States were the dominant hypothesis for the spread of weedy sunflowers in European fields [38,86,87]. As for the wild "ruderal" biotypes, their spread into non–crop areas such as roadsides, water channels, firebreaks, etc., is thought to be promoted by anthropogenic activities [39,85,90,91]. The ruderal biotypes can hybridize recurrently with the domesticated plants leading to the spread of highly competitive hybrids in the field [4,39,92]. Although seed transport by humans is considered to explain the invasion of weedy sunflowers in South America, the role of ruderal biotypes in the spread of weedy forms in these regions and also in North America is highlighted [88,92–94]. For instance, Kane and Rieseberg [94] attributed the development of multiple weedy sunflower populations in the United States to the presence of ruderal populations near cultivated sunflower fields. Several factors favor the hybridization process including the overlapping flowering periods of domesticated and wild sunflower, the self-incompatibility trait of wild sunflower, and the presence of shared pollinators under real field conditions [34]. In addition, pollen transfer from the crop to wild plants can occur even from 1 km away [18].

3.2. Morphological and Ecological Traits

Various forms of *H. annuus* occur as domesticated sunflowers, as weeds in agriculture and as wild plants on naturally disturbed, uncultivated sites. Domesticated sunflowers have unbranched stems of 1.2–2.0 m tall, topped by a single, large-diameter yellow-colored head. In addition, anthocyanins are not present in the plant tissues [83,84]. However, weedy sunflowers have taller stems characterized by apical or full branching. Unlike domesticated plants, weedy sunflowers form several heads per plant, usually between 17 and 34. Head diameter, seeds per head, 1000 seed weight, and seed oil content are significantly lower compared to cultivated sunflowers. Head color can be red or yellow. Anthocyanins are found in the stem, petioles, and stigma. Research has shown that the morphology of weedy sunflowers is intermediate between wild biotypes and domesticated sunflowers [4,13,39,86,88]. The wild trait of self-incompatibility and the domesticated trait of male-sterility can be also observed [34,86].

Seed dormancy is an important ecological trait of weedy sunflowers that enables seed bank formation on agricultural lands. In greenhouse tests conducted by Presotto et al. [17]

with five weedy sunflower populations, seed dormancy reached 77% when no stratification treatments were applied. In another recent study, weedy sunflower seeds remained viable and dormant in the soil for 42 months, suggesting that such biotypes form persistent seedbanks and even establish on agricultural lands outside their native range [20]. Seed dormancy and seedbank formation are traits that originated in wild populations and were transferred to weedy sunflowers through crop–wild hybridization [17,20,86,95,96]. On top of seed dormancy, the seed shattering ability of weedy sunflowers contributes to their success as agricultural weeds. The seeds are easily detached from the heads due to the anatomy of the disks, which are characterized by a lower depth–width ratio compared to domesticated sunflowers, replenishing the seed bank of weedy sunflower in the field [4,92]. As for seed production, it can range between 2200 and 6460 seeds per plant [22,97,98]. Presotto et al. [30] found that the fitness and seed production of weedy sunflowers can be significantly reduced compared to their domesticated and wild parents. However, the same authors found that relative fitness and fertility of plants tended to increase when weedy sunflowers were backcrossed with cultivated or wild sunflower populations.

3.3. Competitive Ability and Distribution

Weedy sunflowers were reported as agricultural weeds in their native range, i.e., in North America, South America and particularly Argentina, and also in several countries in Europe [22,25,86,98,99]. Their competitive ability is attributed to their early-season vigor, rooting, and vegetative growth, plant height, and allelopathic potential [13,100,101]. There are several reports highlighting the detrimental effect of weedy sunflower interference on the yield performance of summer field crops (Table 3).

In the three-year field trials conducted by Casquero et al. [13] in Argentina, sunflower seed yield loss surpassed 50% due to weedy sunflower interference at the density of 4 plants m^{-2}. At higher density, i.e., 10.7 plants m^{-2}, weedy sunflower reduced sunflower seed numbers per plant, 1000 seed weight and seed yield per plant by 66, 41, and 80%, respectively [22]. As for the presence of weedy sunflowers as agricultural weeds in the United States, Deines et al. [26] found that weedy sunflower was 11 times more competitive than shattercane and predicted a yield loss of 46% for maize due to competition from 4 weedy sunflower plants m^{-2}. In the study by Falkenberg et al. [99], competition 20–25 plants m^{-2} reduced maize net return by 66–68% compared to the case where weedy sunflower was controlled by herbicide application. In soybean, the presence of 3 plants m^{-2} reduced seed yield by 47–72% compared to weed-free conditions [24]. Geier et al. [100] noticed that weedy sunflower interference at a density of 4.6 plants m^{-2} resulted in almost complete seed yield loss. In another study, weedy sunflower caused a 94% reduction in seed yield under real–field conditions and reduced soybean height and biomass under greenhouse conditions [101]. In pulse crops, Mesbah et al. [102] observed that 1.5 weedy sunflower plants per m of row reduced the dry bean (*Phaseolus vulgaris* L.) seed yield by 27–34% and also that weedy sunflower was far more competitive than green foxtail (*Setaria viridis* (L.) Beauv.). Moreover, cowpea [*Vigna unguiculata* (L.) Walp.] biomass was reported to decrease by 77–82% in the presence of 6 weeds m^{-2} [28]. In cotton (*Gossypium hirsutum* L.), season-long interference resulted in complete yield loss at densities of 5, 10, 20, and 50 weedy sunflower plants m^{-2} [25]. As for another industrial crop, competition from 6, 12, 18, and 24 plants per 30 m of row was reported to reduce the root yield of sugar beet (*Beta vulgaris* L.) by 40, 52, 67, and 73%, respectively [103]. These authors also found that weedy sunflower was more competitive than velvetleaf (*Abutilon theophrasti* Medic.). In northeastern Mexico, Rosales–Robles et al. [104] recorded a grain yield loss of 27, 49, 60, 71 and 75% for spring wheat (*Triticum aestivum* L.), in the presence of 2, 4, 8, 16, and 32 weedy sunflower plants m^{-2}.

Table 3. Yield losses of summer field crops due to weedy sunflower (*Helianthus annuus* L.) interference. Results presented are from field trials repeated in time or space.

Crop	Weedy Sunflower Density	Yield Loss	Reference
Sunflower	4 Plants m^{-2}	50%	[13]
Sunflower	10.7 Plants m^{-2}	80%	[22]
Sunflower	12–15 Plants m^{-2}	35–60%	[86]
Maize	4 Plants m^{-2}	34%	[26]
Spring Wheat	2–32 Plants m^{-2}	27–75%	[104]
Soybean	3 Plants m^{-2}	47–72%	[24]
Soybean	4.6 Plants m^{-2}	97%	[100]
Soybean	220 Heads m^{-2}	94%	[101]
Dry Bean	1.5 Plants m^{-1} of Row	27–34%	[102]
Cowpea	6 Plants m^{-2}	77–82%	[28]
Cotton	5–50 Plants m^{-2}	100%	[25]
Sugar Beet	6–30 Plants m^{-1} of Row	40–73%	[103]

There is also evidence that weedy sunflower has invaded European fields in recent years. Infestations were observed mainly in the Mediterranean and Balkan Peninsula countries. In France, Muller et al. [86] recorded significant losses in seed yield (35–60%) of sunflower when grown in competition with 12–15 weedy sunflower plants m^{-2}. The same authors found 12 weedy sunflower populations in a total of 300 sunflower fields studied in Andalusia, Spain. In the same prefecture, Poverene and Cantamutto [105] detected weedy sunflower infestations at a density of 5–7 plants per 100 m^2 in a sunflower field and also detected weedy sunflower patches in uncultivated areas near sunflower fields. In Central Italy, weedy sunflower plants were found in sunflower, maize, sugar beet, processing tomato, alfalfa (*Medicago sativa* L.), and tobacco (*Nicotiana tabacum* L.) fields. The most severe infestations were observed on the moist margins of arable fields where tillage and herbicide treatments were limited or absent [106]. There are no official reports of weedy sunflower in Greece. However, farmers have recently complained about the presence of weedy sunflower plants in sunflower fields in the sunflower growing area of Domokos in Central Greece. According to these unofficial descriptions, the weedy plants are present at densities of 3–6 plants m^{-2} and exhibit typical weedy characteristics, such as branching and the formation of multiple heads with smaller diameters compared to cultivated sunflower hybrids (personal communication; unpublished data). Field surveys will be conducted at these sites to further investigate the development of weedy sunflower populations and also to quantify the effects of competition from weedy sunflowers on sunflower productivity under Greek soil and climatic conditions.

Elsewhere in the Balkan Peninsula, Saulic et al. [107] observed three weedy sunflower populations in northern Serbia, and the different populations showed variability in several morphological characteristics. Bozic et al. [108] conducted field experiments at two sites in Central Serbia where weedy sunflower populations occurred. These authors found that crop-to-weed gene flow was possible and depended on flowering time overlap, wind speed and direction, and also on the distance between the domesticated and wild plants. Stojićević et al. [45] demonstrated that weedy sunflower is a highly invasive species in Serbia, occurring at almost 200 sites with sunflower, maize and spring wheat. These authors found heavy infestations at some sites (20–30 plants m^{-2}) and reported that weedy sunflower can produce about 50–100 small-sized heads per plant (10,000–20,000 seeds per plant). Vrbnicanin et al. [98] studied three populations collected from Central Serbia and found that two populations were potentially resistant to nicosulfuron. According to Bozic et al. [108] and Vrbnicanin et al. [98], this species is also considered invasive in Croatia, Romania and Hungary. As for its occurrence on Central Europe, this weed was detected in sunflower fields and adjacent uncultivated areas on Czech Republic [109].

3.4. Herbicide Resistance

In addition to their competitive ability, weedy sunflower populations have developed resistance to several herbicides (Table 4).

Table 4. Cases of herbicide resistance in weedy sunflower [*Helianthus annuus* L.] populations. Results presented are from temporally and spatially replicated dose-response experiments.

Crop	Herbicide	Mode of Action	Chemical Family	Reference
Soybean	Imazethapyr	ALS Inhibitor	Imidazolinone	[110]
Soybean	Imazethapyr Imazamox Thifensulfuron–Methyl Chlorimuron–Ethyl	ALS Inhibitor ALS Inhibitor ALS Inhibitor ALS Inhibitor	Imidazolinone Imidazolinone Sulfonylurea Sulfonylurea	[111]
Soybean	Imazethapyr Imazaquin Imazamox Chlorimuron–Ethyl Cloransulam–Methyl Flumetsulam	ALS Inhibitor ALS Inhibitor ALS Inhibitor ALS Inhibitor ALS Inhibitor ALS Inhibitor	Imidazolinone Imidazolinone Imidazolinone Sulfonylurea Triazolopyrimidine Triazolopyrimidine	[112]
Soybean	Imazethapyr Chlorimuron–Ethyl	ALS Inhibitor ALS Inhibitor	Imidazolinone Sulfonylurea	[113]
Soybean	Imazethapyr Chlorimuron–Ethyl	ALS Inhibitor ALS Inhibitor	Imidazolinone Sulfonylurea	[75]
Maize	Glyphosate	EPSPS Inhibitor	Glycine	[114]
Sunflower	Imazamox	ALS Inhibitor	Imidazolinone	[30]
Sunflower	Imazapyr	ALS Inhibitor	Imidazolinone	[115]

The herbicide–resistant populations may be naturally selected following consecutive applications of herbicides with the same mode of action in a particular field. Resistance may also occur as a result of gene flow between herbicide–tolerant domesticated sunflower and its wild relatives.

3.4.1. Natural Selection of Herbicide–Resistant Weedy Sunflower Populations

In the USA, resistance to imazethapyr was confirmed in a population found in a soybean field treated with this herbicide for seven consecutive years [110]. Baumgart-nen et al. [111] reported that these biotypes exhibited cross-resistance to imazamox, thifensulfuron–methyl, and chlorimuron–ethyl. Allen et al. [112] observed reduced sensitivity to imazethapyr, imazaquin, imazamox, chlorimuron–ethyl, cloransulam–methyl, and flumetsulam. These populations were collected from a soybean field where chlorimuron–ethyl was consecutively applied to control weedy sunflower in the past. White et al. [113] found a population that was 9 and 39 times more resistant to chlorimuron–ethyl and imazethapyr, respectively, compared to a sensitive population. This population was collected from a field where these herbicides were applied for eight years in rotation for the control of weedy sunflowers in soybean. Zelaya and Owen [75] noticed that a population was 36 and 43 times more resistant to imazethapyr and chlorimuron–ethyl, respectively, compared to a sensitive population. In addition, seven weedy sunflower populations were recently reported to have evolved resistance to glyphosate in fields where glyphosate–resistant maize and cotton were planted for several growing seasons [114].

It should be noted that the cases of herbicide resistance mentioned above were reported from the United States. As for Europe, Vrbnicanin et al. [98] collected two sunflower populations in Serbia from fields treated with nicosulfuron in consecutive years. These authors found that the application of nicosulfuron at the recommended field dose had no effect on the relative fitness and fecundity of the two potentially resistant populations. Although this is not an official case where herbicide resistance was confirmed in dose-

response experiments, these results suggest that herbicide-resistant weedy sunflower may be evolving in Europe.

3.4.2. Herbicide Resistance as a Gene–Flow Consequence in *H. annuus*

Following the introduction of "Clearfield" technology, there is increasing consideration of the spread of imidazolinone-resistant weedy sunflowers in the USA and Europe. This technology was developed in 2003 to create sunflower hybrids with resistance to imidazolinone herbicides and to allow farmers to selectively control broadleaf weeds in the crop; imazamox is the only active ingredient registered for this purpose in the USA, while imazamox and imazapyr are approved in Europe [115]. However, there is evidence that these herbicide–resistant sunflower genotypes can successfully interbreed with wild populations that are present near a cultivated field, leading to the creation of imidazolinone-resistant weedy sunflower populations. Resistance to imazamox, for example, was reported by Massinga et al. [116] in the United States, while Presotto et al. [30] confirmed resistance to imazapyr in Argentina. In such populations, seed dormancy is not affected by hybridization. Seed production, although low in some cases, can increase rapidly when weedy sunflowers backcross with domesticated and wild sunflowers [30,98]. Another consequence of backcrossing is the successful transfer of herbicide resistance traits from weedy sunflowers to wild populations. These herbicide-resistant wild populations can encroach on new cultivated sunflower fields, hybridize with the crop, and generate new populations of herbicide-resistant weedy sunflowers [116].

4. Management of Shattercane [*Sorghum bicolor* (L.) Moench subsp. *drummondii*] and Weedy Sunflower (*Helianthus annuus* L.)

4.1. Proactive Strategies

Weed management should initially rely on the introduction of proactive strategies that prevent the spread of weeds to new agricultural lands [117,118]. Although the spread and establishment of these species is primarily facilitated by early seed shattering, late–emerging individuals may reach maturity at crop harvest [4,14]. Given the morphological and phenological overlap between these crops and their weedy relatives, weed seeds may be harvested when crops are harvested, resulting in seed lot contamination. As a result, shattercane and weedy sunflower can enter new sorghum and sunflower fields, respectively, as seed lot contaminants [39,63]. The machines used for seedbed preparation, sowing and harvesting, and threshing of grains and seeds should be carefully cleaned before moving them from one field to another [13,19]. In addition, systematic scouting of sorghum and sunflower fields for early detection of shattercane and weedy sunflower is crucial when weed density is low. When weedy populations are well established, their control is almost impossible [63,86]. Such proactive strategies prevent the spread of both species, their hybridization with domesticated sorghum and sunflower, and mitigate the consequences of gene flow between crops and their weedy relatives [76,119].

Another important measure to prevent gene flow is the management of crop volunteers and feral populations along field margins and in non–crop areas. To define the two terms: volunteers are crop plants derived from the unintentional loss of seeds during harvest [34]. The germination of these seeds creates populations of crop volunteers that can either grow in subsequent crops in the same field or migrate into field margins and adjacent non–crop areas. In the latter case, populations of a domesticated crop that escape from the field, survive, and successfully reproduce in unmanaged ecosystems are referred to as feral populations [33]. Feral sorghum and sunflower populations can successfully interbreed with shattercane and weedy sunflower, respectively, if they are located at the edge of an infested field [3,34]. The gene flow that occurs from feral to weedy individuals can be very problematic. In sorghum and sunflower fields infested with shattercane and weedy sunflower, respectively, gene flow may be reduced or not occur at all if there is no overlap in flowering time between crops and their weedy relatives. In such cases, flowering overlap may occur between feral populations in field margins and weedy populations growing in

the agricultural field. Consequently, gene flow continues to occur. In other words, feral populations derived from volunteer crop plants can potentially serve as genetic bridges for gene transfer between crop plants and their weedy relatives [34].

Herbicide application is the most effective practice to control shattercane and weedy sunflower in field margins and non–crop areas. Glyphosate may be the most effective active ingredient enabling broad spectrum weed control in marginal areas [5]. However, overreliance should be avoided to prevent the development of glyphosate resistant weeds as recently observed in weedy sunflower populations [114]. To maintain its efficacy over time, alternative weed control options in non–crop areas should gain interest. For instance, recent research has shown that natural, environmentally friendly, non–selective herbicides can be effective on annual weeds if applied repeatedly in early weed growth stages [120].

4.2. Reactive Strategies

Once shattercane and weedy sunflower infestations are observed on agricultural land, reactive strategies for their management include the use of cultural practices, herbicides, and mechanical methods. Effective weed management is essential to avoid yield loss in a variety of summer field crops (including sorghum and sunflower) and also to prevent crop–weed gene flow in sorghum and sunflower fields.

4.2.1. Cultural Practices

Crop rotation is a cultural practice that increases crop diversity in an agricultural area since a series of crops are sequentially grown over time on the same land. In crop rotation systems, crop mimics such as shattercane are subjected to diverse agronomic practices and are affected by alterations in fundamental crop management practices, i.e., tillage, fertilization, irrigation regimes becoming less adaptable and competitive [121]. In addition, crop rotation is accompanied by the rotation of herbicides with different modes of action delaying the selection of herbicide-resistant populations [122]. The importance of crop rotation for the management of shattercane and weedy sunflower was highlighted in the case studies by Werle et al. [63] and Presotto et al. [30], respectively. Diversifying the corn-soybean rotation with cool-season crops such as winter wheat (*Triticum aestivum* L.) and canola (*Brassica napus* L.) resulted in significantly lower weedy sunflower infestation in the study by Anderson [123] especially under no-till conditions.

Growing a cover crop before the establishment of the main cash crop is another cultural practice that can be used for shattercane and weedy sunflower suppression. In the study by Whalen et al. [124] where shattercane was one of the dominant weeds in a soybean field, a cover crop mixture of cereal rye (*Secale cereale* L.) and hairy vetch (*Vicia villosa* Roth) resulted in 83% lower weed biomass; weed suppression increased when the use of cover crops was combined with the application of pre–emergence herbicides with soil residual activity. Sunn hemp (*Crotolaria juncea* L.) is a cover crop with aggressive growth recently reported to have suppressed weedy sunflower emergence and growth in the subsequent cash crop [125]. Intercropping, narrow row spacing, increased seeding rates, fertilization, and irrigation management should also be investigated for the suppression of shattercane and weedy sunflower. There is evidence that such practices contribute to weed management in summer field crops where shattercane and weedy sunflower are troublesome weeds [126–130]. The selection of competitive hybrids and cultivars was also reported to suppress shattercane in maize and weedy sunflowers in summer legumes such as cowpea [28,64]. In addition, the biological cycle of a particular crop genotype may result in no flowering overlap between the crop and its weedy relatives. Therefore, hybrid and cultivar selection may be an option to prevent crop–weed gene flow in sorghum and sunflower. The same is noted for manipulations in crop sowing dates [3,119].

The preparation of a firm seedbed, the use of germinable crop seed, sowing date and sowing depth selection are also cultural practices ensuring optimal crop growth and can lead to the suppression of noxious weeds such as shattercane and weedy sunflower [117]. False seedbed is another cultural, non–chemical, practice recommended for the control of

shattercane and weedy sunflower in a great variety of summer crops including sorghum and sunflower. To apply this practice, the conventional tillage practices used for seedbed preparation are not followed by crop establishment. On the contrary, weeds are left to emerge. At this time, irrigations are encouraged because they stimulate greater weed emergence. After approximately 2 weeks, when the main flush of emergence has passed, weeds are controlled by shallow tillage. Weed control is followed by crop sowing [131]. If shattercane and weedy sunflower populations continue to occur, they can be controlled by subsequent cultivations between crop rows [132].

4.2.2. Herbicides and Mechanical Methods

The strong botanical ties between crops and their weedy relatives precludes, in most cases, selective herbicide use to control shattercane in sorghum fields and weedy sunflower in sunflower fields. The selective control of shattercane and weedy sunflower is possible only when "Inzen" sorghum and "Clearfield" sunflower are treated with ALS-inhibiting herbicides. However, crop–wild gene flow is very likely to result in the spread of herbicide-resistant hybrids in the field [30,63]. In any case, herbicide application is more preferable to be carried out before crop sowing under the concept of stale seedbed. Stale seedbed includes the same actions as false seedbed apart from the weed control method. In stale seedbeds, weed control is carried out by the application of a non–selective herbicide [131]. Both glyphosate and pelargonic acid, a natural contact type non–selective herbicide, have been recently reported to provide sufficient control of annual weeds in summer crops [133].

There are more selective herbicide options in crops which are not genetically related to shattercane and weedy sunflower. However, herbicides with different modes of action should be rotated or applied in mixtures to avoid the development of herbicide-resistant populations [118]. As for mechanical methods, cultivation between crop rows can effectively control both species [134,135]. Mechanical operations may need to be repeated; a general recommendation is to increase the number of interrow cultivations to increase the efficacy of mechanical weed control [126]. There is also evidence that multiple mowing operations between crop rows can also provide solutions in shattercane control [136]. The same author denoted that mowing can be effectively combined with herbicide application. Such practices should also be tested against weedy sunflower.

5. Conclusions

Shattercane and weedy sunflower are two examples of CWRs that have become troublesome weeds in agriculture. Key weedy characteristics such as early seed shattering and seed dormancy play an important role in their success as agricultural weeds. Both species are very competitive to their closely related domesticated crops. Moreover, they can cause severe yield losses in a wide variety of summer field crops. Both species are widely reported as important agricultural weeds in the United States and have invaded various agricultural areas in Europe. Resistance to herbicides was confirmed in both shattercane and weedy sunflower populations. Crop rotation, false seedbed, cover crops, and competitive crop genotypes are valuable cultural practices for suppressing both species. In addition, preventative measures should be also adopted to avoid their spread to new agricultural land. The development of effective weed management strategies is also essential to prevent hybridization between sorghum, sunflower and their wild relatives and mitigate its consequences.

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References

1. Maxted, N.; Ford-Lloyd, B.V.; Jury, S.; Kell, S.; Scholten, M. Towards a definition of a crop wild relative. *Biodivers. Conserv.* **2006**, *15*, 2673–2685. [CrossRef]
2. Ananda, G.K.S.; Myrans, H.; Norton, S.L.; Gleadow, R.; Furtado, A.; Henry, R.J. Wild sorghum as a promising resource for crop improvement. *Front. Plant Sci.* **2020**, *11*, 1108. [CrossRef] [PubMed]
3. Ohadi, S.; Hodnett, G.; Rooney, W.; Bagavathiannan, M. Gene flow and its consequences in *Sorghum* spp. *Crit. Rev. Plant Sci.* **2017**, *36*, 367–385. [CrossRef]
4. Presotto, A.; Fernández-Moroni, I.; Poverene, M.; Cantamutto, M. Sunflower crop-wild hybrids: Identification and risks. *Crop Prot.* **2011**, *30*, 611–616. [CrossRef]
5. Travlos, I.S.; Montull, J.M.; Kukorelli, G.; Malidza, G.; Dogan, M.N.; Cheimona, N.; Antonopoulos, N.; Kanatas, P.J.; Zannopoulos, S.; Peteinatos, G. Key aspects on the biology, ecology and impacts of johnsongrass [*Sorghum halepense* (L.) Pers] and the role of glyphosate and non-chemical alternative practices for the management of this weed in Europe. *Agronomy* **2019**, *9*, 717. [CrossRef]
6. Honsdorf, N.; March, T.J.; Berger, B.; Tester, M.; Pillen, K. High-throughput phenotyping to detect drought tolerance QTL in wild barley introgression lines. *PLoS ONE* **2014**, *9*, e97047.
7. Munns, R.; James, R.A.; Xu, B.; Athman, A.; Conn, S.J.; Jordans, C.; Byrt, C.S.; Haere, R.A.; Tyerman, S.D.; Tester, M.; et al. Wheat grain yield on saline soils is improved by an ancestral Na$^+$ transporter gene. *Nat. Biotechnol.* **2012**, *30*, 360–364. [CrossRef]
8. Zhou, Y.L.; Uzokwe, V.N.E.; Zhang, C.H.; Cheng, L.R.; Wang, L.; Chen, K.; Gao, X.Q.; Sun, Y.; Chen, J.J.; Zhu, L.H.; et al. Improvement of bacterial blight resistance of hybrid rice in China using the *Xa23* gene derived from wild rice (*Oryza rufipogon*). *Crop Prot.* **2011**, *30*, 637–644. [CrossRef]
9. Hu, D.; Zhang, H.; Du, Q.; Hu, Z.; Yang, Z.; Li, X.; Wang, J.; Huang, F.; Yu, D.; Wang, H.; et al. Genetic dissection of yield-related traits via genome-wide association analysis across multiple environments in wild soybean (*Glycine soja* Sieb. and Zucc.). *Planta* **2020**, *251*, 1–17. [CrossRef]
10. Capel, C.; Del Carmen, A.F.; Alba, J.M.; Lima-Silva, V.; Hernández-Gras, F.; Salinas, M.; Boronat, A.; Angosto, T.; Botella, M.A.; Fernández-Muñoz, R.; et al. Wide-genome QTL mapping of fruit quality traits in a tomato RIL population derived from the wild-relative species *Solanum pimpinellifolium* L. *Theor. Appl. Genet.* **2015**, *128*, 2019–2035. [CrossRef]
11. Swamy, B.M.; Sarla, N. Yield-enhancing quantitative trait loci (QTLs) from wild species. *Biotechnol. Adv.* **2008**, *26*, 106–120. [CrossRef] [PubMed]
12. Kaya, Y.; Jocic, S.; Miladinovic, D. Sunflower. In *Technological Innovations in Major World Oil Crops*; Gupta, S.K., Ed.; Springer: New York, NY, USA, 2012; Volume 1, pp. 85–129.
13. Casquero, M.; Presotto, A.; Cantamutto, M. Exoferality in sunflower (*Helianthus annuus* L.): A case study of intraspecific/interbiotype interference promoted by human activity. *Field Crops Res.* **2013**, *142*, 95–101. [CrossRef]
14. Defelice, M.S. Shattercane, *Sorghum bicolor* (L.) Moench ssp. *drummondii* (Nees ex Steud.) De Wet ex Davidse—Black sheep of the family. *Weed Technol.* **2006**, *20*, 1076–1083.
15. Nadir, S.; Xiong, H.-B.; Zhu, Q.; Zhang, X.-L.; Xu, H.-Y.; Li, J.; Dongchen, W.; Henry, D.; Guo, X.-Q.; Khan, S. Weedy rice in sustainable rice production. A review. *Agron. Sustain. Dev.* **2017**, *37*, 46. [CrossRef]
16. Ejeta, G.; Grenier, C. Sorghum and its weedy hybrids. In *Crop Ferality and Volunteerism*; Gressel, J., Ed.; CRC Press: Boca Raton, FL, USA, 2005; pp. 123–135.
17. Presotto, A.; Poverene, M.; Cantamutto, M. Seed dormancy and hybridization effect of the invasive species, *Helianthus annuus*. *Ann. Appl. Biol.* **2014**, *164*, 373–383. [CrossRef]
18. Arias, D.M.; Rieseberg, L.H. Gene flow between cultivated and wild sunflowers. *Theor. Appl. Genet.* **1994**, *89*, 655–660. [CrossRef] [PubMed]
19. Chauhan, B.S. Strategies to manage weedy rice in Asia. *Crop Prot.* **2013**, *48*, 51–56. [CrossRef]
20. Presotto, A.; Hernández, F.; Casquero, M.; Vercellino, R.; Pandolfo, C.; Poverene, M.; Cantamutto, M. Seed bank dynamics of an invasive alien species, *Helianthus annuus* L. *J. Plant Ecol.* **2020**, *13*, 313–322. [CrossRef]
21. Schmidt, J.J.; Yerka, M.K.; Pedersen, J.F.; Lindquist, J.L. Growth, fitness, and overwinter survival of a shattercane (*Sorghum bicolor* ssp. *drummondii*) × grain sorghum (*Sorghum bicolor* ssp. *bicolor*) F$_2$ population. *Weed Sci.* **2018**, *66*, 634–641.
22. Casquero, M.; Cantamutto, M. Interference of the agrestal *Helianthus annuus* biotype with sunflower growth. *Weed Res.* **2016**, *56*, 229–236. [CrossRef]
23. Werle, R.; Bernards, M.L.; Sattler, S.E.; Lindquist, J.L. Susceptibility of shattercane × ALS-resistant sorghum hybrids and their parents to rimsulfuron and nicosulfuron. In Proceedings of the 53rd Annual Meeting of Weed Science Society of America, Baltimore, MD, USA, 4–7 February 2013; Weed Science Society of America: Champaign, IL, USA, 2013. Abstract 331.
24. Allen, J.R.; Johnson, W.G.; Smeda, R.J.; Kremer, R.J. ALS resistant *Helianthus annuus* interference in *Glycine max*. *Weed Sci.* **2000**, *48*, 461–466. [CrossRef]

25. Charles, G.W.; Sindel, B.M.; Cowie, A.L.; Knox, O.G. Determining the critical period for weed control in high-yielding cotton using common sunflower as a mimic weed. *Weed Technol.* **2019**, *33*, 800–807. [CrossRef]

26. Deines, S.R.; Dille, J.A.; Blinka, E.L.; Regehr, D.L.; Staggenborg, S.A. Common sunflower (*Helianthus annuus*) and shattercane (*Sorghum bicolor*) interference in corn. *Weed Sci.* **2004**, *52*, 976–983. [CrossRef]

27. Raey, Y.; Ghassemi-Golezani, K.; Javanshir, A.; Alyari, H.; Mohammadi, S.A. Interference between shattercane (*Sorghum bicolor*) and soybean (*Glycine max*). *N. Z. J. Crop Hortic. Sci.* **2005**, *33*, 53–58. [CrossRef]

28. Wang, G.; McGiffen, M.E.; Ehlers, J.D.; Marchi, E.C. Competitive ability of cowpea genotypes with different growth habit. *Weed Sci.* **2006**, *54*, 775–782. [CrossRef]

29. Heap, I. The International Herbicide-Resistant Weed Database. Available online: www.weedscience.org (accessed on 2 September 2021).

30. Presotto, A.; Ureta, M.S.; Cantamutto, M.; Poverene, M. Effects of gene flow from IMI resistant sunflower crop to wild *Helianthus annuus* populations. *Agric. Ecosyst. Environ.* **2012**, *146*, 153–161. [CrossRef]

31. Werle, R.; Schmidt, J.J.; Laborde, J.; Tran, A.; Creech, C.F.; Lindquist, J.L. Shattercane × ALS-tolerant sorghum F_1 hybrid and shattercane interference in ALS-tolerant sorghum. *J. Agric. Sci.* **2014**, *6*, 159–165. [CrossRef]

32. Ellstrand, N.C.; Prentice, H.C.; Hancock, J.F. Gene flow and introgression from domesticated plants into their wild relatives. *Annu. Rev. Ecol. Evol. Syst.* **1999**, *30*, 539–563. [CrossRef]

33. Gressel, J. Introduction—The challenges of ferality. In *Crop Ferality and Volunteerism*; Gressel, J., Ed.; CRC Press: Boca Raton, FL, USA, 2005; pp. 1–7.

34. Reagon, M.; Snow, A.A. Cultivated *Helianthus annuus* (Asteraceae) volunteers as a genetic "bridge" to weedy sunflower populations in North America. *Am. J. Bot.* **2006**, *93*, 127–133. [CrossRef]

35. Engku, A.K.; Norida, M.; Juraimi, A.S.; Rafii, M.Y.; Abdullah, S.N.A.; Alam, M.A. Gene flow from Clearfield® rice to weedy rice under field conditions. *Plant Soil Environ.* **2016**, *62*, 16–22.

36. Sahoo, L.; Schmidt, J.J.; Pedersen, J.F.; Lee, D.J.; Lindquist, J.L. Growth and fitness components of wild × cultivated *Sorghum bicolor* (Poaceae) hybrids in Nebraska. *Am. J. Bot.* **2010**, *97*, 1610–1617. [CrossRef] [PubMed]

37. Schmidt, J.J.; Pedersen, J.F.; Bernards, M.L.; Lindquist, J.L. Rate of shattercane × sorghum hybridization in situ. *Crop Sci.* **2013**, *53*, 1677–1685. [CrossRef]

38. Faure, N.; Serieys, H.; Bervillé, A. Potential gene flow from cultivated sunflower to volunteer, wild *Helianthus* species in Europe. *Agric. Ecosyst. Environ.* **2002**, *89*, 183–190. [CrossRef]

39. Ureta, M.S.; Carrera, A.D.; Cantamutto, M.A.; Poverene, M.M. Gene flow among wild and cultivated sunflower, *Helianthus annuus* in Argentina. *Agric. Ecosyst. Environ.* **2008**, *123*, 343–349. [CrossRef]

40. Taiz, L.; Zeiger, E.; Moller, I.M.; Murphy, A. *Plant Physiology and Development*, 6th ed.; Sinauer Associates: Sunderland, CT, USA, 2015.

41. Taylor, L.P.; Hepler, P.K. Pollen germination and tube growth. *Annu. Rev. Plant Biol.* **1997**, *48*, 461–491. [CrossRef] [PubMed]

42. Steinhorst, L.; Kudla, J. Calcium—A central regulator of pollen germination and tube growth. *Biochim. Biophys. Acta* **2013**, *1833*, 1573–1581. [CrossRef] [PubMed]

43. Zheng, R.H.; Su, S.D.; Xiao, H.; Tian, H.Q. Calcium: A Critical factor in pollen germination and tube elongation. *Int. J. Mol. Sci.* **2019**, *20*, 420. [CrossRef]

44. Berenji, J.; Dahlberg, J. Perspectives of sorghum in Europe. *J. Agron. Crop Sci.* **2004**, *190*, 332–338. [CrossRef]

45. Stojićević, D.; Ilić, A.; Sekulić, T.; Stupar, V.; Božić, D.; Vrbničanin, S. Distribution of weedy sunflower on territory of Republic of Serbia and potential risks for agriculture. *J. Hortic. For. Biotechnol.* **2017**, *21*, 132–137.

46. De Wet, J.M.J. Systematics and evolution of *Sorghum* Sect. *Sorghum* (Gramineae). *Am. J. Bot.* **1978**, *65*, 477–484. [CrossRef]

47. Harlan, J.R.; de Wet, J.M.J. A simplified classification of cultivated sorghum. *Crop Sci.* **1972**, *12*, 172–176. [CrossRef]

48. Wiersema, J.H.; Dahlberg, J. The nomenclature of *Sorghum bicolor* (L.) Moench (Gramineae). *Taxon* **2007**, *56*, 941–946. [CrossRef]

49. Beckett, T.H.; Stoller, E.W.; Wax, L.M. Interference of four annual weeds in corn (*Zea mays*). *Weed Sci.* **1988**, *36*, 764–769. [CrossRef]

50. Dille, J.A.; Stahlman, P.W.; Thompson, C.R.; Bean, B.W.; Soltani, N.; Sikkema, P.H. Potential yield loss in grain sorghum (*Sorghum bicolor*) with weed interference in the United States. *Weed Technol.* **2020**, *34*, 624–629. [CrossRef]

51. Hans, S.R.; Johnson, W.G. Influence of shattercane [*Sorghum bicolor* (L.) Moench.] interference on corn (*Zea mays* L.) yield and nitrogen accumulation. *Weed Technol.* **2002**, *16*, 787–791. [CrossRef]

52. Celarier, R.P. Cytotaxonomic notes on the subsection *Halepensia* of the genus *Sorghum*. *Bull. Torrey Bot. Club* **1958**, *85*, 49–62. [CrossRef]

53. Paterson, A.H.; Schertz, K.F.; Lin, Y.R.; Liu, S.C.; Chang, Y.L. The weediness of wild plants: Molecular analysis of genes influencing dispersal and persistence of johnsongrass, *Sorghum halepense* (L.) Pers. *Proc. Natl. Acad. Sci. USA* **1995**, *92*, 6127–6131. [CrossRef] [PubMed]

54. Dillon, S.L.; Lawrence, P.K.; Henry, R.J.; Price, H.J. *Sorghum* resolved as a distinct genus based on combined ITS1, ndh F and Adh 1 analyses. *Plant Syst. Evol.* **2007**, *268*, 29–43. [CrossRef]

55. Klein, P.; Smith, C.M. Invasive johnsongrass, a threat to native grasslands and agriculture. *Biologia* **2021**, *76*, 413–420. [CrossRef]

56. Quinby, J.R.; Karper, R.E. Inheritance of height in sorghum. *Agron. J.* **1954**, *46*, 211–216. [CrossRef]

57. Horak, M.J.; Moshier, L.J. Shattercane (*Sorghum bicolor*) biology and management. *Rev. Weed Sci.* **1994**, *6*, 133–149.

58. Burnside, O.C.; Wicks, G.A.; Fenster, C.R. Longevity of shattercane seed in soil across Nebraska. *Weed Res.* **1977**, *17*, 139–143. [CrossRef]
59. Fellows, G.M.; Roeth, F.W. Factors influencing shattercane (*Sorghum bicolor*) seed survival. *Weed Sci.* **1992**, *40*, 434–440. [CrossRef]
60. Adugna, A.; Bekele, E. Morphology and fitness components of wild × crop F1 hybrids of *Sorghum bicolor* (L.) in Ethiopia: Implications for survival and introgression of crop genes in the wild pool. *Plant Genet. Resour.* **2013**, *11*, 196–205. [CrossRef]
61. Vesecky, J.F.; Feltner, K.C.; Vanderlip, R.L. Wild cane and forage sorghum competition in grain sorghum. *Weed Sci.* **1973**, *21*, 28–32. [CrossRef]
62. King, S.R.; Hagood, E.S. Herbicide programs for the control of ALS-resistant shattercane (*Sorghum bicolor*) in corn (*Zea mays*). *Weed Technol.* **2006**, *20*, 416–421. [CrossRef]
63. Fellows, G.M.; Roeth, F.W. Shattercane (*Sorghum bicolor*) interference in soybean (*Glycine max*). *Weed Sci.* **1992**, *40*, 68–73. [CrossRef]
64. Hoffman, M.L.; Buhler, D.D. Utilizing sorghum as a functional model of crop-weed competition. I. Establishing a competitive hierarchy. *Weed Sci.* **2002**, *50*, 466–472. [CrossRef]
65. Werle, R.; Tenhumberg, B.; Lindquist, J.L. Modeling shattercane dynamics in herbicide-tolerant grain sorghum cropping systems. *Ecol. Modell.* **2017**, *343*, 131–141. [CrossRef]
66. Schaffasz, A.; Windpassinger, S.; Friedt, W.; Snowdon, R.; Wittkop, B. Sorghum as a novel crop for Central Europe: Using a broad diversity set to dissect temperate-adaptation. *Agronomy* **2019**, *9*, 535. [CrossRef]
67. Popescu, A. Sorghum production in the EU–28 in the period 2008–2019 and its forecast for 2020–2014 horizon. *Sci. Pap. Ser. Manag. Econ. Eng. Agric. Rural. Dev.* **2020**, *20*, 479–488.
68. United States Department of Agriculture (USDA). Weed Risk Assessment for *Sorghum bicolor* (L.) Moench Nothosubsp. *drummondii* (Steud.) de Wet ex Davidse (Poaceae). Available online: https://www.aphis.usda.gov/plant_health/plant_pest_info/weeds/downloads/wra/sorghum-bicolor-drummondii.pdf (accessed on 18 September 2021).
69. Dahlberg, J.; Berenji, J.; Sikora, V.; Latković, D. Assessing sorghum [*Sorghum bicolor* (L.) Moench] germplasm for new traits: Food, fuels & unique uses. *Maydica* **2012**, *56*, 85–92.
70. Schwartz-Lazaro, L.M.; Gage, K.L. Sustainable weed control in grain sorghum. In *Weed Control: Sustainability, Hazards, and Risks in Cropping Systems Worldwide*; Korres, N.E., Burgos, N.R., Duke, S.O., Eds.; CRC Press: Boca Raton, FL, USA, 2018; pp. 262–275.
71. Berenji, J.; Dahlberg, J.; Sikora, V.; Latkovi, D. Origin, history, morphology, production, improvement, and utilization of broomcorn [*Sorghum bicolor* (L.) Moench] in Serbia. *Econ. Bot.* **2011**, *65*, 190–208. [CrossRef]
72. Anderson, D.D.; Roeth, F.W.; Martin, A.R. Discovery of a primisulfuron-resistant shattercane (*Sorghum bicolor*) biotype. *Weed Technol.* **1998**, *12*, 74–77. [CrossRef]
73. Lee, C.D.; Martin, A.R.; Roeth, F.W.; Johnson, B.E.; Lee, D.J. Comparison of ALS inhibitor resistance and allelic interactions in shattercane accessions. *Weed Sci.* **1999**, *47*, 275–281. [CrossRef]
74. Brenly-Bultemeier, T.L.; Stachler, J.; Harrison, S.K. Confirmation of shattercane (*Sorghum bicolor*) resistance to ALS-inhibiting herbicides in Ohio. *Plant Health Prog.* **2002**, *3*, 1. [CrossRef]
75. Zelaya, I.A.; Owen, M.D.K. Evolved resistance to acetolactate synthase-inhibiting herbicides in common sunflower (*Helianthus annuus*), giant ragweed (*Ambrosia trifida*), and shattercane (*Sorghum bicolor*) in Iowa. *Weed Sci.* **2004**, *52*, 538–548. [CrossRef]
76. Werle, R.; Jhala, A.J.; Yerka, M.K.; Dille, J.A.; Lindquist, J.L. Distribution of herbicide-resistant shattercane and johnsongrass populations in sorghum production areas of Nebraska and Northern Kansas. *Agron. J.* **2016**, *108*, 321–328. [CrossRef]
77. Mutegi, E.; Sagnard, F.; Labuschagne, M.; Herselman, L.; Semagn, K.; Deu, M.; de Villiers, S.; Kanyenji, B.M.; Mwongera, N.; Traore, P.C.S.; et al. Local scale patterns of gene flow and genetic diversity in a crop-wild-weedy complex of sorghum (*Sorghum bicolor* (L.) Moench) under traditional agricultural field conditions in Kenya. *Conserv. Genet.* **2012**, *13*, 1059–1071. [CrossRef]
78. Magomere, T.O.; Obukosia, S.D.; Shibairo, S.I.; Ngugi, E.K.; Mutitu, E. Evaluation of relative competitive ability and fitness of *Sorghum bicolor* × *Sorghum halepense* and *Sorghum bicolor* × *Sorghum sudanense* F₁ hybrids. *J. Biol. Sci.* **2015**, *15*, 1–15. [CrossRef]
79. Tuinstra, M.R.; Al-Khatib, K. Acetolactate Synthase Herbicide Resistant Sorghum. U.S. Patent Application 20080216187, 4 September 2008.
80. Schilling, E.E. Helianthus. In *Flora of North America*; Flora of North America Editorial Committee, Ed.; Oxford University Press: New York, NY, USA; Oxford, UK, 2006; Volume 21, pp. 141–169.
81. Stebbins, J.C.; Winchell, C.J.; Constable, J.V.H. *Helianthus winteri* (Asteraceae), a new perennial species from the southern Sierra Nevada foothills, California. *Aliso* **2013**, *31*, 19–24. [CrossRef]
82. Timme, R.E.; Simpson, B.B.; Linder, C.R. High-resolution phylogeny for *Helianthus* (Asteraceae) using the *18S–26S* ribosomal DNA external transcribed spacer. *Am. J. Bot.* **2007**, *94*, 1837–1852. [CrossRef] [PubMed]
83. Heiser, C.B., Jr. Taxonomy of *Helianthus* and origin of domesticated sunflower. In *Sunflower Science and Technology*; Carter, J.F., Ed.; American Society of Agronomy, Crop Science Society of America, Soil Science Society of America: Madison, WI, USA, 1978; Agronomy Monographs; Volume 19, pp. 31–53.
84. Heiser, C.B., Jr. Variation and subspeciation in the common sunflower, *Helianthus annuus*. *Am. Midl. Nat.* **1954**, *51*, 287–305. [CrossRef]
85. Cantamutto, M.; Poverene, M. The transgenic sunflower. In *Genetics, Genomics and Breeding of Sunflower*; Hu, J.G., Seiler, G., Kole, C., Eds.; Science Publishers: Enfield, CT, USA, 2010; pp. 279–312.

86. Muller, M.H.; Delieux, F.; Fernandez-Martinez, J.M.; Garric, B.; Lecomte, V.; Anglade, G.; Leflon, M.; Motard, C.; Segura, R. Occurrence, distribution and distinctive morphological traits of weedy *Helianthus annuus* L. populations in Spain and France. *Genet. Resour. Crop Evol.* **2009**, *56*, 869–877. [CrossRef]

87. Muller, M.H.; Latreille, M.; Tollon, C. The origin and evolution of a recent agricultural weed: Population genetic diversity of weedy populations of sunflower (*Helianthus annuus* L.) in Spain and France. *Evol. Appl.* **2011**, *4*, 499–514. [CrossRef]

88. Presotto, A.; Hernández, F.; Díaz, M.; Fernández-Moroni, I.; Pandolfo, C.; Basualdo, J.; Cuppari, S.; Cantamutto, M.; Poverene, M. Crop-wild sunflower hybridization can mediate weediness throughout growth-stress tolerance trade-offs. *Agric. Ecosyst. Environ.* **2017**, *249*, 12–21. [CrossRef]

89. Lincoln, R.J.; Boxshall, G.A.; Clarck, P.F. *A Dictionary of Ecology, Evolution and Systematics*, 2nd ed.; Cambridge University Press: Cambridge, UK, 1998.

90. Cantamutto, M.; Torres, L.; Presotto, A.; Gutierrez, A.; Ureta, S.; Poverene, M. Migration pattern suggested by terrestrial proximity as possible origin of wild annual *Helianthus* populations in central Argentina. *Biol. Invasions* **2010**, *12*, 541–551. [CrossRef]

91. Poverene, M.; Cantamutto, M.; Seiler, G.J. Ecological characterization of wild *Helianthus annuus* and *Helianthus petiolaris* germplasm in Argentina. *Plant Genet. Resour.* **2009**, *7*, 42–49. [CrossRef]

92. Burke, J.M.; Gardner, K.A.; Rieseberg, L.H. The potential for gene flow between cultivated and wild sunflower (*Helianthus annuus*) in the United States. *Am. J. Bot.* **2002**, *89*, 1550–1552. [CrossRef] [PubMed]

93. Cantamutto, M.; Presotto, A.; Moroni, I.F.; Alvarez, D.; Poverene, M.; Seiler, G. High infraspecific diversity of wild sunflowers (*Helianthus annuus* L.) naturally developed in central Argentina. *Flora* **2010**, *205*, 306–312. [CrossRef]

94. Kane, N.C.; Rieseberg, L.H. Genetics and evolution of weedy *Helianthus annuus* populations: Adaptation of an agricultural weed. *Mol. Ecol.* **2008**, *17*, 384–394. [CrossRef]

95. Alexander, H.M.; Schrag, A.M. Role of soil seed banks and newly dispersed seeds in population dynamics of the annual sunflower, *Helianthus annuus*. *J. Ecol.* **2003**, *91*, 987–998. [CrossRef]

96. Moody-Weis, J.; Alexander, H.M. The mechanisms and consequences of seed bank formation in wild sunflowers (*Helianthus annuus*). *J. Ecol.* **2007**, *95*, 851–864. [CrossRef]

97. Mercer, K.L.; Wyse, D.L.; Shaw, R.G. Effects of competition on the fitness of wild and crop-wild hybrid sunflower from a diversity of wild populations and crop lines. *Evolution* **2006**, *60*, 2044–2055. [CrossRef]

98. Vrbnicanin, S.P.; Bozic, D.M.; Pavlovic, D.M.; Saric-Krsmanovic, M.M.; Stojicevic, D.; Uludag, A. Fitness studies on invasive weedy sunflower populations from Serbia. *Rom. Biotechnol. Lett.* **2017**, *22*, 12464–12472.

99. Falkenberg, N.R.; Cogdill, T.J.; Rister, M.E.; Chandler, J.M. Economic evaluation of common sunflower (*Helianthus annuus*) competition in field corn. *Weed Technol.* **2012**, *26*, 137–144. [CrossRef]

100. Geier, P.W.; Maddux, L.D.; Moshier, L.J.; Stalman, P.W. Common sunflower (*Helianthus annuus*) interference in soybean (*Glycine max*). *Weed Technol.* **1996**, *16*, 787–791. [CrossRef]

101. Irons, S.M.; Burnside, O.C. Competitive and allelopathic effects of sunflower (*Helianthus annuus*). *Weed Sci.* **1982**, *30*, 372–377. [CrossRef]

102. Mesbah, A.O.; Miller, S.D.; Koetz, P.J. Common sunflower (*Helianthus annuus*) and green foxtail (*Setaria viridis*) interference in dry bean. *Weed Technol.* **2004**, *18*, 902–907. [CrossRef]

103. Schweizer, E.E.; Bridge, L.D. Sunflower (*Helianthus annuus*) and velvetleaf (*Abutilon theophrasti*) interference in sugarbeets (*Beta vulgaris*). *Weed Sci.* **1982**, *30*, 514–519. [CrossRef]

104. Rosales-Robles, E.; Salinas-García, J.R.; Sánchez-de-la-Cruz, R.; Rodríguez-del-Bosque, L.A.; Esqueda-Esquivel, V. Interference and control of wild sunflower (*Helianthus annuus* L.) in spring wheat (*Triticum aestivum* L.) in northeastern México. *Cereal Res. Commun.* **2002**, *30*, 439–446. [CrossRef]

105. Poverene, M.; Cantamutto, M. A comparative study of invasive *Helianthus annuus* populations in their natural habitats of Argentina and Spain. *Helia* **2010**, *33*, 63–74. [CrossRef]

106. Vischi, M.; Cagiotti, M.E.; Cenci, C.A.; Seiler, G.J.; Olivieri, A.M. Dispersal of wild sunflower by seed and persistant basal stalks in some areas of Central Italy. *Helia* **2006**, *29*, 89–94. [CrossRef]

107. Saulic, M.; Stojicevic, D.; Matkovic, A.; Bozic, D.; Vrbnicanin, S. Population variability of weedy sunflower as invasive species. In Proceedings of the 4th ESENIAS Workshop: International Workshop on IAS in Agricultural and Non-Agricultural Areas in ESENIAS Region, Çanakkale, Turkey, 16–17 December 2013; Uludağ, A., Trichkova, T., Tomov, R., Eds.; Çanakkale Onsekiz Mart University, Turkey—East and South European Network for Invasive Alien Species (ESENIAS)—Institute of Biodiversity and Ecosystem Research, BAS, Bulgaria: Çanakkale, Turkey, 2013; pp. 79–85.

108. Bozic, D.; Pavlovic, D.; Bregola, V.; Di Loreto, A.; Bosi, S.; Vrbnicanin, S. Gene flow from herbicide-resistant sunflower hybrids to weedy sunflower. *J. Plant Dis. Prot.* **2015**, *122*, 183–188. [CrossRef]

109. Holec, J.; Soukup, J.; Cerovska, M.; Novakova, K. Common sunflower (*Helianthus annuus* var. *annuus*)—Potential threat to coexistence of sunflower crops in Central Europe. In Proceedings of the 2nd European Conference on Co-Existence between GM and Non-GM Based Agricultural Supply Chain, Montpellier, France, 14–15 November 2005; Messean, S., Ed.; Agropolis Productions: Montpellier, France, 2005; pp. 271–272.

110. Al-Khatib, K.; Baumgartner, J.R.; Peterson, D.E.; Currie, R.S. Imazethapyr resistance in common sunflower (*Helianthus annuus*). *Weed Sci.* **1998**, *46*, 403–407. [CrossRef]

111. Baumgartner, J.R.; Al-Khatib, K.; Currie, R.S. Cross-resistance of imazethapyr-resistant common sunflower (*Helianthus annuus*) to selected imidazolinone, sulfonylurea, and triazolopyrimidine herbicides. *Weed Technol.* **1999**, *13*, 489–493. [CrossRef]

112. Allen, J.R.; Johnson, W.G.; Smeda, R.J.; Wiebold, W.J.; Massey, R.E. Management of acetolactate synthase (ALS)–resistant common sunflower (*Helianthus annuus* L.) in soybean (*Glycine max*). *Weed Technol.* **2001**, *15*, 571–575. [CrossRef]

113. White, A.D.; Owen, M.D.; Hartzler, R.G.; Cardina, J. Common sunflower resistance to acetolactate synthase-inhibiting herbicides. *Weed Sci.* **2002**, *50*, 432–437. [CrossRef]

114. Singh, V.; Etheredge, L.; McGinty, J.; Morgan, G.; Bagavathiannan, M. First case of glyphosate resistance in weedy sunflower (*Helianthus annuus*). *Pest Manag. Sci.* **2020**, *76*, 3685–3692. [CrossRef]

115. Tan, S.; Evans, R.R.; Dahmer, M.L.; Singh, B.K.; Shaner, D.L. Imidazolinone-tolerant crops: History, current status and future. *Pest Manag. Sci.* **2005**, *61*, 246–257. [CrossRef]

116. Massinga, R.A.; Al-Khatib, K.; Amand, P.S.; Miller, J.F. Gene flow from imidazolinone-resistant domesticated sunflower to wild relatives. *Weed Sci.* **2003**, *51*, 854–862. [CrossRef]

117. Gazoulis, I.; Kanatas, P.; Papastylianou, P.; Tataridas, A.; Alexopoulou, E.; Travlos, I. Weed management practices to improve establishment of selected lignocellulosic crops. *Energies* **2021**, *14*, 2478. [CrossRef]

118. Norsworthy, J.K.; Ward, S.M.; Shaw, D.R.; Llewellyn, R.S.; Nichols, R.L.; Webster, T.; Bradley, K.; Frisvold, G.; Powles, S.; Burgos, N.R.; et al. Reducing the risks of herbicide resistance: Best management practices and recommendations. *Weed Sci.* **2012**, *60*, 31–62. [CrossRef]

119. Roumet, M.; Noilhan, C.; Latreille, M.; David, J.; Muller, M.-H. How to escape from crop-to-weed gene flow: Phonological variation and isolation-by-time within weedy sunflower population. *New Phytol.* **2013**, *197*, 642–654. [CrossRef] [PubMed]

120. Kanatas, P.; Antonopoulos, N.; Gazoulis, I.; Travlos, I.S. Screening glyphosate-alternative weed control options in important perennial crops. *Weed Sci.* **2021**, 1–15. [CrossRef]

121. Reeves, D.W. Cover crops and rotations. In *Crops Residue Management (Advances in Soil Science)*, 1st ed.; Hatfield, J.L., Stewart, B.A., Eds.; Lewis Publishers: Boca Raton, FL, USA, 1994; pp. 125–172.

122. Kanatas, P. Mini-Review: The role of crop rotation, intercropping, sowing dates and increased crop density towards a sustainable crop and weed management in arable crops. *Agraarteadus* **2020**, *31*, 22–27.

123. Anderson, R.L. Crop sequence and no-till reduce seedling emergence of common sunflower (*Helianthus annuus*) in following years. *Weed Technol.* **2007**, *21*, 355–358. [CrossRef]

124. Whalen, D.M.; Shergill, L.S.; Kinne, L.P.; Bish, M.D.; Bradley, K.W. Integration of residual herbicides with cover crop termination in soybean. *Weed Technol.* **2020**, *34*, 11–18. [CrossRef]

125. Soti, P.; Racelis, A. Cover crops for weed suppression in organic vegetable systems in semiarid subtropical Texas. *Org. Agric.* **2020**, *10*, 429–436. [CrossRef]

126. Kanatas, P.J.; Gazoulis, I. The integration of increased seeding rates, mechanical weed control and herbicide application for weed management in chickpea (*Cicer arietinum* L.). *Phytoparasitica* **2021**, 1–13. [CrossRef]

127. Kanatas, P.; Gazoulis, I.; Travlos, I. Irrigation timing as a practice of effective weed management in established alfalfa (*Medicago sativa* L.) crop. *Agronomy* **2021**, *11*, 550. [CrossRef]

128. Kanatas, P.; Travlos, I.; Kakabouki, I.; Papastylianou, P.; Gazoulis, I. Yield of organically grown maize hybrids as affected by two green manure crops in Greece. *Chil. J. Agric. Res.* **2020**, *80*, 334–341. [CrossRef]

129. Iqbal, N.; Manalil, S.; Chauhan, B.S.; Adkins, S.W. Effect of narrow row-spacing and weed crop competition duration on cotton productivity. *Arch. Agron. Soil Sci.* **2020**, 1–13. [CrossRef]

130. Rad, S.V.; Valadabadi, S.A.R.; Pouryousef, M.; Saifzadeh, S.; Zakrin, H.R.; Mastinu, A. Quantitative and qualitative evaluation of *Sorghum bicolor* L. under intercropping with legumes and different weed control methods. *Horticulturae* **2020**, *6*, 78. [CrossRef]

131. Travlos, I.; Gazoulis, I.; Kanatas, P.; Tsekoura, A.; Zannopoulos, S.; Papastylianou, P. Key factors affecting weed seeds' germination, weed emergence, and their possible role for the efficacy of false seedbed technique as weed management practice. *Front. Agron.* **2020**, *2*, 1. [CrossRef]

132. Del Pino, A.M.; Pannacci, E.; Di Michele, A.; Bravi, E.; Marconi, O.; Tei, F.; Palmerini, C.A. Selective inhibition of wild sunflower reproduction with mugwort aqueous extract, tested on cytosolic Ca^{2+} and germination of the pollen grains. *Plants* **2021**, *10*, 1364. [CrossRef] [PubMed]

133. Kanatas, P.; Travlos, I.; Papastylianou, P.; Gazoulis, I.; Kakabouki, I.; Tsekoura, A. Yield, quality and weed control in soybean crop as affected by several cultural and weed management practices. *Not. Bot. Horti Agrobot. Cluj-Napoca* **2020**, *48*, 329–341. [CrossRef]

134. Burnside, O.C. Shattercane control in narrow-row soybeans. *Agron. J.* **1980**, *72*, 753–757. [CrossRef]

135. Muller, M.H.; Lecomte, V.; Garric, B.; Jouffret, P.; Leflon, M.; Pourageaux, F.; Ségura, R. Weedy sunflowers in France: Prevalence and first inferences on their origin. In Proceedings of the 17th International Sunflower Conference, Cordoba, Spain, 8–12 June 2008; pp. 685–690.

136. Donald, W.W. Control of both winter annual and summer annual weeds in no-till corn with between-row mowing systems. *Weed Technol.* **2007**, *21*, 591–601. [CrossRef]