



Review

# Herbicide Resistance and Management Options of *Papaver rhoeas* L. and *Centaurea cyanus* L. in Europe: A Review

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**Abstract:** Corn poppy (*Papaver rhoeas* L.) and cornflower (*Centaurea cyanus* L.) are two overwintering weed species found in crop fields in Europe. They are characterised by a similar life cycle, similar competitive efforts, and a spectrum of herbicides recommended for their control. This review summarises the biology and herbicide resistance phenomena of corn poppy and cornflower in Europe. Corn poppy is one of the most dangerous dicotyledonous weeds, having developed herbicide resistance to acetolactate synthase inhibitors and growth regulators, especially in Mediterranean countries and Great Britain. Target site resistance to acetolactate synthase inhibitors dominates among herbicide-resistant poppy biotypes. The importance of non-target site resistance to acetolactate synthase inhibitors in this species may be underestimated because non-target site resistance is very often associated with target site resistance. Cornflower, meanwhile, is increasingly rare in European agricultural landscapes, with acetolactate synthase inhibitors-resistant biotypes only listed in Poland. However, the mechanisms of cornflower herbicide resistance are not well recognised. Currently, herbicides mainly from acetolactate synthase and photosystem II inhibitors as well as from synthetic auxins groups are recommended for the control of both weeds. Integrated methods of management of both weeds, especially herbicide-resistant biotypes, continue to be underrepresented.

**Keywords:** ALS-resistance; herbicides; mechanisms of resistance; fitness; integrated weed management

## 1. Introduction

Corn poppy (*Papaver rhoeas* L.) and cornflower (*Centaurea cyanus*, L.) are two species of annual, dicotyledonous weeds that have a similar biological cycle. Corn poppy is one of the best-known species of the genus *Papaver*, which is most frequently represented in the Papaveraceae family [1–3]. Cornflower belongs to the family Asteraceae, one of the most numerous among vascular plants [4].

There are several factors that can affect changes in weed populations, such as soil cultivation, crop rotation, fertilisation and irrigation. However, herbicide use is associated with rapid evolution of herbicide resistance. The application of herbicides is presently a key management strategy in horticultural and agronomic crops. Currently, around 150 chemical compounds are used against weeds, representing 25 different sites of action in all [5]. This relatively small variation in the site of action can lead to multi-family resistance over time.

In modern agriculture, herbicide-resistant (HR) weeds are a worldwide phenomenon. The intensive use of herbicides, primarily since the 1980s, has led to a selection of weeds that is resistant. The definition of herbicide resistance given by the Herbicide Resistance Action Committee (HRAC) is “the natural ability of a weed biotype to survive an application of a herbicide that would normally kill it” [6]. This phenomenon has significant environmental implications, such as reduced biodiversity, while its economic constraints include a decrease in crop yield quantity and quality. Moreover, the control of resistant weeds requires the use of additional herbicides with varying sites of action, or higher use rates. Several authors point to HR corn poppy as Europe’s most important resistant dicotyledonous weed [7–10], with just two monocotyledonous weeds above it: *Alopecurus myosuroides* Huds. (blackgrass) and *Lolium* sp. (ryegrass). According to Calha et al. [10] and Rey-Caballero et al. [11], an increase in cereal monoculture farming and the overuse of 2,4-Dichlorophenoxyacetic acid (2,4-D) (since the 1960s) followed by tribenuron-methyl application (in the early 1980s) have selected acetolactate synthase (ALS) inhibitors and/or 2,4-D resistant biotypes of corn poppy. In contrast, cornflower is characterised by sensitivity to high herbicide pressure [12]. The International Survey of Herbicide-Resistant Weeds [13] as well as Adamczewski et al. [14] have recorded a low number of herbicide-resistant cornflower biotypes that are found in Poland only. The identification of the mechanism of resistance—target site or non-target site—in a certain weed population of corn poppy and cornflower is very useful for making responsible weed management decisions [15].

The presence of resistant poppy and cornflower in fields poses a significant threat to the quantity and quality of crop yields as well as to the biodiversity of accompanying weed communities. Therefore, the resistant populations should be managed by implementing several integrated weed management strategies, both conventional ones and those that are underrepresented [15]. Recommended management strategies should be preceded by a resistance risk assessment. As specified in the European and Mediterranean Plant Protection Organization (EPPO) Standard PP 1/213, this consists of an evaluation of the herbicide’s inherent and agronomic risk [16]. The inherent risk is assessed using the characteristics of both the herbicide’s active ingredient(s) and the target weed species. For the target weeds, consideration is given to both the biological characteristics that may predispose a weed species to evolve resistance (such as the length of lifecycle, seed production, distribution and longevity, and genetic plasticity), and the extent to which resistance has already been found in that species.

Moss et al. [17] provide a list of weed species of high or medium inherent risk of evolving resistance. *P. rhoeas* is qualified as a high-risk species. *C. cyanus* is not included in this list and therefore should be considered a low-risk species. It is important to recognise that the actual species included within such a risk analysis will differ considerably depending on the region of the world and that the categorisation process will change over time as resistance is confirmed in additional species [17]. However, even a weed species with a low risk of evolving resistance can become a problem and cornflower is one such example.

Both corn poppy and cornflower are annual dicotyledonous weeds; they often infest winter crops and there are many similarities in the types of herbicides used for their successful control. However, their actual distribution and the frequency of herbicide-resistant biotypes differ. Therefore, it is of

interest to compare these species, their biology and the history of their control, all of which have led to the present situation in Europe.

The aims of this review are to characterise (i) the biology and status of HR corn poppy (*Papaver rhoeas* L.) and cornflower (*Centaurea cyanus* L.) in Europe; (ii) the chemical control of both weed species in the last five decades in Europe; and (iii) their selection for herbicide resistance and management options.

## 2. Biology and Distribution of Corn Poppy and Cornflower

Corn poppy is widespread across Europe [18,19], predominantly in central and southern regions, with lower frequencies in northern Europe [20]. It is also found in Asia, North and South America, South Africa, Australia and Oceania [2,3,21,22]. Cornflower is found in various locations in Europe (Figure 1) and Asia, and has also been introduced to North America, where it is considered an invasive species [4,23–29]. Both species are noticeable due to the intense red or crimson colour of the corn poppy flowers [3], and the intense blue of cornflower [30] (Figure 1).

The development of herbicide resistance in weeds is determined by the species' biological characteristics. Annual weeds that have a short life cycle and reproduce generatively are specifically prone to evolve herbicide resistance [31,32], and this is true of both corn poppy and cornflower. In temperate climates, they belong to the group of what are known as overwintering weeds, which means that they can emerge in the autumn or spring. In the early stages of growth, they form a leaf rosette (Figure 1A,B), while in the generative phase of growth, they form erect shoots ending with a single flower (poppy) or inflorescence (cornflower) [18] (Figure 1C,D). Both species only reproduce annually by seed, bloom and produce seeds within the upper layers of the crop canopy (Figure 1E,F), and shed seeds before or during crop harvesting, thus increasing the capacity of the soil weed seed bank [4,33]. The challenge presented by the establishment of corn poppy is associated with its high fecundity, with seeds that retain long-term dormancy in soil [2,25,33–35]. According to Cirujeda et al. [36], following storage in soil for 77 months, the viability of corn poppy seeds was on average 62%. In the case of cornflower, it also displays a high reproductive effort, especially in dense stands, and moreover, is able to maximise its fertility in adverse soil conditions [37]. However, the viability of cornflower seeds in soil is very low, with less than 10% viability after 36 months of storage [12].

Corn poppy and cornflower are frequently found in similar types of agroecosystems [38], mainly winter cereals [39], where they are also more fertile [34]. Corn poppy dominates in winter wheat, where it causes the greatest yield losses. In some countries, it is also a serious weed in winter barley, rye and winter oilseed rape. It can also occur in spring crops such as oats or legumes as well as in sugar beet and non-cultivated areas [2,3,34,40,41]. Cornflower is a weed of agronomic crops. It is mostly associated with winter cereals, including rye [4,42], and in recent years, its frequency has increased in winter oilseed rape [38,43]. On rare occasions, it is also found in spring cereals, root crops and legumes [44].

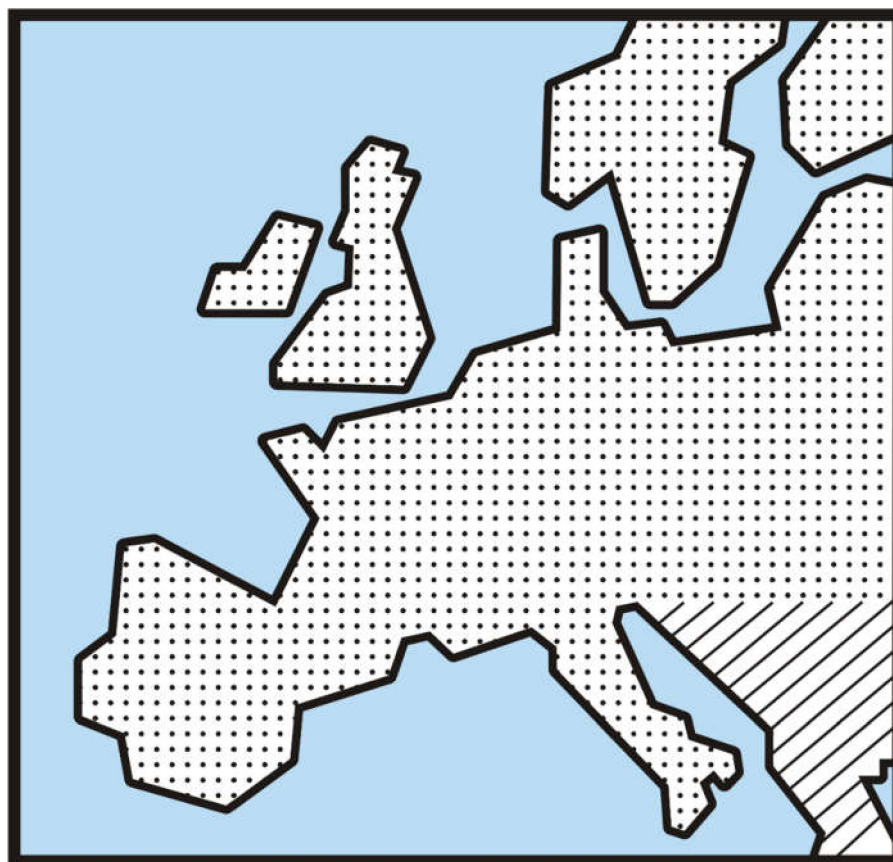




**Figure 1.** Leaf rosette of corn poppy (A) and cornflower (B). Flower of corn poppy (C) and inflorescence of cornflower (D). Corn poppy (E) and cornflower (F) blooming in the winter cereals. Photo credit: Prof. K. Domaradzki.

Both corn poppy and cornflower are strong competitors with crops [2,3,34,45,46]. The presence of corn poppy or cornflower in a canopy can reduce the winter wheat yield by 12–37% [45–47]. Cornflower is also more competitive than other weed species in a multi-species canopy [48]. In recent decades, there have been clear disparities in the frequencies of corn poppy and cornflower on Europe’s agricultural landscape. Corn poppy is widespread throughout Europe, whereas cornflower is becoming increasingly rare (Figure 2). This change in status may be associated with the genotypic and phenotypic diversity of each of these weeds, correlated with, among other things, a pollination pattern. Both corn poppy and cornflower are insect pollinated. However, corn poppy is highly

self-compatible; it exhibits significant genetic variation and a high phenotypic plasticity, which cause variable coloration of the crown petals and variable leaf shapes [49,50]. Genetic diversity in corn poppy populations indicates its high potential for adaptation to changing environmental conditions and its ability to settle new habitats [51,52]. In contrast, cornflower is a self-incompatible, and thus, cross-pollinating species [25,26]. Apidae insects play a significant role in its reproduction [53]. It is believed that a recent decrease in the number of wild pollinators has led to an inbreeding depression of this species, which has significantly reduced the fitness of individuals [26,53]. The resultant low level of genetic differentiation between populations and a fine-scale spatial genetic structure within populations suggest limited local dispersal [48]. Moreover, progress in agronomic practices, especially high inputs of nitrogen, herbicidal intensification and the use of certified crop seeds, is also a significant reason for the decline in cornflower frequency in many European countries [4,12,25,26,35,54–56]. Thus, in western Europe, the cornflower has become a rare species and an indicator of biodiversity in arable fields [4,57–59]. In Sweden, it is typically found on organic farms [60]. Natural cornflower populations in the British Isles are becoming less common. There are ornamental varieties of this species, grown in home gardens and public spaces, which are becoming sources of weeds for ruderal habitats [61]. However, in some other countries, especially in central Europe, there is an increase in the frequencies of cornflower populations again [62], causing strong competitive pressure with crops and other weed species [63]. For example, in the Czech Republic, cornflower populations have been restored in the last three decades, mainly due to the increase in winter oilseed rape cropping [43,57,62]. This is also the case in Poland [64,65] and northern Germany [66,67]. In the southeastern part of Poland, the frequency of cornflower in fields has remained high. This has been facilitated by the structure of farms, where most arable land is on sandy and acidic soils [68,69].



**Figure 2.** Distribution of *Centaurea cyanus* (L.) in Europe. Legend: lines—the species is widespread; dots—the species is present, but less frequent. Source: reference [18].

### 3. Revision of Herbicides for Controlling Corn Poppy and Cornflower in Europe

Herbicide resistance is induced by a selective pressure of the herbicides used by farmers [70]. The intensity of this phenomenon is driven both by the herbicides' chemical diversity and their different sites of action, their availability on the market, and their popularity among farmers related to their price. A combination of these may increase or slow down the selection of HR individuals and the development of HR populations [71].

This review tracked the availability of active ingredients (a.i.) registered in the last 50 years against corn poppy and cornflower on the European (EU) market (Tables 1 and 2) using the Pesticide Manual [72].

Recently, the number of herbicides available on the EU market has decreased substantially due to Council Directive 91/414/EEC of 15 July 1991, with a derogation as defined in Article 4 Clause 7 of Regulation No 1107/2009, i.e., the reduction in active substances of importance in agriculture due to environmental constraints [73]. Consequently, the following substances, previously used against poppy and cornflower, were withdrawn from the market: cyanazine (2004), simazine (2008), prometryne (2008), oxadiargyl (2010) and isoproturon (2016). Meanwhile, the market launch of new herbicides to control both species has been a much rarer event.

Presently, the list contains 25 major active ingredients recommended against corn poppy, which means that the loss of substances is not particularly substantial compared with their availability in the 1970s (Table 1). However, the qualitative changes related to the recommended herbicides are more important. Of these, the a.i. in the HRAC groups B, C1 and O for control of corn poppy dominate, but the number of a.i. with a lower risk of developing resistance has decreased. On the EU market, 30% and 9% of a.i. registered against corn poppy are found in groups B and C1, respectively (Table 1). Herbicides from these groups are classified as those that have a high risk of developing resistant weeds, especially among those species or genera that are more prone to the selection of herbicide resistance, i.e., corn poppy [17]. It should be noted that the majority of the C1 ingredients used against corn poppy were withdrawn from the market, with only chloridazon and lenacil still available (Table 1).

**Table 1.** List of active ingredients in herbicides recommended (red colour) for controlling *Papaver rhoeas* L. in Europe in the period 1970–2020.

SoA <sup>1</sup> (HRAC)	Active Ingredient	1970–1980	1981–1990	1991–2000	2001–2010	2011–2020
B	chlorosulfuron					
	florasulam					
	iodosulfuron-methyl-Na					
	metsulfuron-methyl					
	rimsulfuron					
	tribenuron-methyl					
C1	thifensulfuron-methyl					
	chloridazon					
	cyanazine					
	lenacil					
	prometryne					
C1 + K3	simazine					
	phenmedipham + ethofumesate					
C2	isoproturon					
E	oxadiargyl					
F1	flurochloridone					
F1 + K3	diflufenican + flufenacet					
F2 + B	tembotrione +					
	thiencarbazone-methyl					
K1	propyzamide					
K3	metazachlor					
O	aminopyralid					
	clopyralid					
	dicamba					
	MCPA					
	MCPB					
	mecoprop					

<sup>1</sup> SoA—site of action, HRAC – Herbicide Resistance Action Committee; Source: reference [72].



Herbicides from HRAC O group, which have a medium resistance risk [17], constitute 26% of all a.i. currently recommended for use against corn poppy in the EU.

Similarly, as for corn poppy, herbicides that have a high risk of developing resistance [17] also dominate in the list of herbicides for controlling cornflower. Currently, the European market offers herbicides with a total of 25 a.i., which is just two a.i. fewer than those registered since the 1970s (Table 2). The a.i. from HRAC B and C1 together constitute 41% of all a.i. against cornflower. Unlike corn poppy, however, cornflower was classified as a weed with a low risk of developing herbicide resistance in Europe [17]. According to Håkansson [74], the widespread use of herbicides from the group of phenoxy acids and sulfonylureas is one of the main reasons for the decrease in the number of cornflowers in Europe.

**Table 2.** List of active ingredients in herbicides recommended (blue colour) for controlling *Centaurea cyanus* L. in Europe and in Poland in the period 1970–2020.

SoA <sup>1</sup> (HRAC)	Active Ingredient	1970–1980	1981–1990	1991–2000	2001–2010	2011–2020
B	chlorsulfuron					
	flupyrsulfuron-methyl					
	iodosulfuron-methyl-Na					
	metsulfuron-methyl					
	rimisulfuron					
	tribenuron-methyl					
	tritosulfuron + florasulam					
C1	cyanazine					
	metamitron					
	metribuzin					
C2	chlorotoluron					
C3	bentazon					
	bromoxynil					
E	oxadiargyl					
F1	diflufenikan					
F2 + B	tembotrione + thiencazone-methyl					
K1 + C2	pendimethalin + isoproturon					
O	2,4-D <sup>2</sup>					
	aminopyralid					
	clopyralid					
	dicamba					
	fluroxypyr					
	MCPA					
	MCPB					

<sup>1</sup> SoA—site of action, HRAC – Herbicide Resistance Action Committee; <sup>2</sup> 2,4-D - 2,4-Dichlorophenoxyacetic acid; Source: [72].

From the active ingredients registered in the EU for the control of corn poppy and cornflower, 33% of them can be used to control both species. Almost all the active ingredients present a systemic type of action, which means that they are taken up by the plant (roots or leaves) and can act in the distant organs [75]. Furthermore, a.i. that are taken up by both leaves and roots (67%) dominate over those taken up exclusively by leaves (31%). The management of HR weeds involves, among other things, the use of herbicides with two or more sites of action in the growing season, and these can be applied in the control of corn poppy and cornflower. Moreover, growers can use active substances for which only a few cases of resistance have been found, such as chlorotoluron or diflufenican.

Several authors have shown that mixtures of herbicides effectively reduce and slow the development of herbicide resistance [71,76,77]. In practice, the herbicides from HRAC group O (e.g., 2,4-D, MCPA, clopyralid, dicamba) are widely used for preparing mixtures with other a.i., for example, with sulfonylureas. The use of such herbicide mixtures can lead to a reduction in herbicide-resistant populations of both cornflower and corn poppy.

In summary, the EU market for herbicides to control corn poppy and cornflower is dominated by herbicides from the HRAC B and HRAC O groups. These a.i. are classified as having a high (HRAC B) or medium (HRAC O) risk of developing resistance [17]. Diversification of active substances in the control of cornflower and corn poppy is possible in practice, which offers good prospects for limiting the spread of herbicide-resistant biotypes.

#### 4. Characteristics of Herbicide-Resistant Corn Poppy

Herbicide-resistant corn poppy is the most important broadleaved weed in Europe and the number of new cases of HR biotypes for this species is still growing [78,79]. Many biotypes of HR corn poppy originate from southern European countries such as Greece, Italy and Spain; however, this problem also concerns other European countries such as Belgium, Denmark, France, Germany, Poland, Sweden and the United Kingdom [13]. Table 3 features a list of papers on HR corn poppy biotypes published in the past 20 years.

The testing of corn poppy resistance to herbicides in the cited studies included the application of classical biological methods, i.e., a dose-response test with a calculation of resistance index (RI), which is the ratio of an effective dose (ED50) causing a 50% reduction in the measured parameter (usually fresh/dry leaf weight or visual assessments of injury/mortality of the resistant biotype (ED50<sub>R</sub>)) in relation to the similar parameter reduction in a reference sensitive biotype (ED50<sub>S</sub>). Among the tests confirming the corn poppy's resistance to 2,4-D was also a seed-based quick test, based on the ratio of the mean length of coleoptiles in test populations compared with the susceptible standard [79]. HR populations were classified as susceptible to 2,4-D if the coleoptile length ratios were 1, a low degree of resistance was shown by a length ratio of between 1 and 1.5, a middle degree of resistance had a ratio of between 1.5 and 2.0, and a high degree of resistance had a ratio greater than 2 [79].

The majority of papers included corn poppy resistant to herbicides from the ALS inhibitors group (HRAC B/2). Among these, tribenuron-methyl resistance predominates [80]. Tribenuron-methyl is an active substance of the family of sulfonylurea herbicides, which has been available on European markets since 1986 [81]. The second, less frequent group was corn poppy biotypes selected for resistance to the synthetic auxins (HRAC O/4), mainly 2,4-D, which acts in plants in a similar way to indolyl-3-acetic acid. 2,4-D is one of the most widely used herbicides and has been available on the market since 1945 [82]. Significant also is a selection of corn poppy biotypes with multiple resistance to different herbicides of the sulfonylurea group and also 2,4-D or MCPA [11,50,83]. Kotoula-Syka et al. [84] identified a poppy biotype from Bafra (north Greece) that was highly resistant to chlorsulfuron, but also cross-resistant to tribenuron, triasulfuron, thifensulfuron and imazethapyr. In southwest Poland, field screening was conducted on 179 fields from 2000 to 2005 [85]. This identified the presence of corn poppy resistant to herbicides from the group of inhibitors of photosynthesis at photosystem II (HRAC C1), which was confirmed by dose-response tests as well as by changes in chlorophyll *a* fluorescence in the poppy leaves. On the monitored fields, three cases of cross-resistance were also found: two poppy biotypes resistant to atrazine and simazine, three biotypes resistant to atrazine and metamitron, and three biotypes resistant to atrazine and bentazone [85].



**Table 3.** Characteristics of herbicide-resistant biotypes of *Papaver rhoeas* from Europe (published data).

Country	Biotype	Herbicide	HRAC <sup>1</sup> Group	RI <sup>2</sup>	Test	TSR/NTSR <sup>5</sup>	Ref.
Spain	25/98	chlorosulfuron, metsulfuron, rimsulfuron, sulfometuron, tribenuron,	B/2	n.a. <sup>3</sup>	ALS activity test	TSR	[86]
Spain	CU1 CU2	imazamox, imazapyr 2,4-D 2,4-D and tribenuron 2,4-D, dicamba and aminopyralid	O/4 O/4, B/2	n.a.	Seed-based quick test	NTSR	[79,83]
Spain	D-R703 F-R213	2,4-D and tribenuron, dicamba and aminopyralid	O/4 O/4, B/2	15 12 and 286	DRT <sup>4</sup>	NTSR	[11]
Spain	R-213 R-313 R-114 R-703	tribenuron florasulam imazamox 2,4-D	B/2, O/4	2–695 2–24 6–40 12–18	DRT	TSR NTSR	[87]
Greece	28 biotypes from Thessaloniki, Kilkis and Serres	tribenuron pyrithiobac imazamox florasulam	B/2 B/2 B/2 B/2	from 137 to >2400 from 12.4 to >88 from 1.5 to 28.3 from 5.6 to 25.4	DRT	TSR	[88–90]
Greece	Bafra	chlorsulfuron tribenuron triasulfuron thifensulfuron	B/2 B/2 B/2 B/2	149 149 99 >>400	DRT	TSR	[84]
Italy	9 biotypes	tribenuron	B/2	n.a.	whole-plant pot test-field rate	TSR	[91]
Italy	02-24, 02-26 * 04-38, 04-41, 04-44	tribenuron imazamox florasulam	B/2 B/2 B/2	n.a.	whole-plant pot test-field rate	TSR, NTSR *	[92,93] *
France, Greece, Italy, Spain United Kingdom	over 20 populations	metsulfuron tribenuron 2,4-D	B/2 B/2 O/4	n.a.	whole-plant pot test-dose 1N and 2N	TSR (ALS inhibitors)	[50]
		metsulfuron	B/2	n.a.	DRT	n.a.	[94]
United Kingdom	DEV001, DEV002 DK001	metsulfuron; tribenuron; MCPA metsulfuron; tribenuron metsulfuron; tribenuron	B/2; O/4 B/2 B/2	>18; n.a.; 1.8 >18; n.a. >18; n.a.	DRT	TSR	[9]
Poland	40% resistant out of 179 collected	atrazine, simazine, cyanazine and metamitron isoproturon, bentazone	C1 C2	>6	DRT and fluorescence test	n.a.	[85]
Poland	R1 R2	tribenuron	B2	26 24	DRT	n.a.	[95]

<sup>1</sup> HRAC—Herbicide Resistance Action Committee; <sup>2</sup> RI—resistance index; <sup>3</sup> n.a.—not assessed; <sup>4</sup> DRT—dose-response test; <sup>5</sup> TSR/NTSR—target site/non-target site resistance; \* NTSR mechanism of population 02-26 has been studied in depth by Scarabel et al. [93].

Herbicide-resistant corn poppy biotypes showed varying values of RI (Table 3). In the case of resistance to herbicides from HRAC O/4, RI values ranged from 1.8 (resistance to MCPA) to 18 (resistance to 2,4-D). Biotypes highly resistant to tribenuron (HRAC group B/2) were found in Greece, ranging from RI = 137 for the least resistant to RI greater than 2400 for the most resistant poppy biotypes [88]. However, Délye et al. [92] screened a total of 729 individual poppy plants for resistance to B/2 herbicides, but without calculating their resistance index. Of the 201 plants classified as tribenuron-resistant, 9% of plants were moderately resistant, with dead leaves around rosettes and regrowth of fresh leaves from their centre, which could be referred to as a Phoenix effect [96]. Of the 193 plants classified as imazamox-resistant, 7.8% of plants were moderately resistant. In contrast, of the 71 plants classified as florasulam-resistant, 63.4% of plants were moderately resistant [92]. Kati et al. [50] studied the frequency of resistant poppy biotypes in populations from Greece, Italy, Spain and France. Resistance to ALS inhibitors was detected in 24 of the 27 field populations assayed. In Greek populations, the frequencies of resistance to iodosulfuron + mesosulfuron ranged from 4% to 53%. In Italian and French populations, the frequencies of resistance to tribenuron ranged from 77% to 88% and 15% to 100%, respectively. The frequency of resistance to metsulfuron in Spanish populations ranged from 52.5% to 100%. Resistance to 2,4-D was observed in 25 of the 27 field populations assayed. Overall, plants resistant to ALS inhibitors were observed with plants resistant to 2,4-D in seven populations from Greece, five from Italy, eight from France and three from Spain. The study of Kati et al. [50]

demonstrated for the first time the occurrence of multiple resistance to ALS inhibitors and to auxinic herbicides in individual corn poppy plants in these countries.

In some of the HR corn poppy biotypes listed above, there have been no studies of the herbicide resistance mechanism [85,94,95] or it has only been studied for the selected herbicides, i.e., for ALS inhibitors, but not for 2,4-D [50]. For those where the mechanism of resistance was studied, in the case of biotypes resistant to herbicides from the HRAC B/2 group, a target site resistance (TSR) dominated [9,50,84,86,88]. The TSR mechanisms largely involve mutation(s) in a herbicide's target site of action, resulting in an insensitive or less sensitive target protein of the herbicide [97]. The majority of biotypes showing this resistance mechanism are characterised by high RI values [88]. In the case of three HR poppy biotypes from the UK, they possessed ALS gene point mutations (Pro-197-Leu or Pro-197-His), conferring resistance to the sulfonylurea herbicides metsulfuron and tribenuron-methyl [9]. In the case of five Italian populations, six mutant ALS alleles—namely Pro-197-Arg, Pro-197-His, Pro-197-Leu, Pro-197-Ser, Pro-197-Thr, and Trp-574-Leu—were identified [92]. Mutations in codon 197 have also been identified in French and Spanish populations [50,86]. Nucleotide variation around codon 197 indicates that mutant ALS alleles evolved by multiple, independent appearances [92]. Mutations in codon 574 have been found less frequently, but mutations in codons 197 and 574 have been reported in one of the French corn poppy populations [50]. Different alleles of the ALS gene can be found in the same population of corn poppy or in the same plant [92]. A comparison of individual plant phenotype and genotype (non-synonymous mutations at codon 197) showed that all mutant ALS alleles conferred dominant resistance to the field dose of the sulfonylurea tribenuron, and moderate or no resistance to the field dose of the triazolopyrimidine florasulam. In Spanish populations, mutation Pro-197-Ser has been identified, conferring high resistance to sulfonylureas and imidazolinones, except imazethapyr. ALS isolated from resistant plants from this population seem to be more sensitive to imazethapyr than ALS isolated from sensitive plants. Herbicide–enzyme interactions are probably very complex and different mutations in ALS genes can affect the binding of each herbicide molecule differently, thus influencing patterns of cross-resistance to other ALS inhibitors [86].

Saari et al. [98] identified that most of the species resistant to ALS inhibitors are a result of the presence of a single nuclear gene with incomplete dominance. TSR is a common mechanism of resistance in corn poppy, however, resistance to ALS inhibitors in this species can be also due to a non-target site resistance (NTSR) mechanism, which usually results from an enhanced metabolism of herbicide [87,92,93]. The importance of NTSR to ALS inhibitors may well be underestimated in broadleaved weeds, possibly because it is very often associated with TSR [92]. Scarabel et al. [93] investigated the occurrence, inheritance and genetic control of NTSR to tritosulfuron (sulfonylureas), imazamox (imidazolinones) and florasulam (triazolopyrimidines) in corn poppy. Their results suggest that NTSR is polygenic and loci with moderate individual effects in single plants are gradually accumulated over generations. Metabolism studies with imazamox have confirmed the presence of enhanced metabolism in at least one Spanish population [87]. Both TSR and NTSR mechanisms to ALS-inhibiting herbicides can coexist in the same population or even in an individual corn poppy plant [87,92,93].

In biotypes with 2,4-D resistance in corn poppy, the only proposed explanation for this is the NTSR mechanism [11,83]. To date, NTSR mechanisms, which include reduced herbicide uptake, reduced translocation and detoxification, are recognised as being the main type of resistance mechanism to 2,4-D (herbicide group O) in weeds [99]. Recently, cell death has also been discovered as an NTSR mechanism [100]. Weed species can show one or more mechanisms within NTSR to synthetic auxins and, as Palma-Bautista et al. [101] demonstrate in their study of six different dicotyledonous weeds resistant to 2,4-D, extrapolating the mechanism from one weed species to another is very risky. The molecular mechanisms of NTSR in weeds remain to be elucidated. TSR to auxinic herbicides is much less frequent; it has been recently been reported in *Kochia scoparia* (L.) [102]. Among other factors, the rarity of TSR mechanisms described so far in weeds can be explained by the potential multiple sites of action of synthetic auxins [99].

In the resistant biotypes of corn poppy from Spain, non-target site resistance was related to a reduced translocation of 2,4-D from treated leaves to the rest of the plant, leading to an eight-fold lower ethylene production by the resistant plants compared with the susceptible ones [11]. In the same biotypes, an enhanced metabolism of 2,4-D was confirmed as a mechanism of resistance by the presence of two hydroxy metabolites in the shoots and roots of the resistant biotypes [83]. The authors hypothesise that a malathion inhibiting P450 is responsible for the formation of the hydroxy metabolites detected in the tests. The relationship between impaired translocation and enhanced metabolism remains unclear and requires investigation [83]. One of the hypotheses proposed is that reduced translocation might be a secondary effect of enhanced metabolism [101]. Based on qPCR, within five hours of herbicide application, Scarabel et al. [103] detected an increase in GH3 (indole-3-acetic acid amido synthetase) and GST3 (glutathione S-transferase)—two genes upregulated following 2,4-D treatment—confirming their involvement in plant response to 2,4-D. The GH3 expression level was similar in susceptible and 2,4-D-resistant corn poppy plants, confirming that this response is not related to the plants' resistance status. In the study of Scarabel et al. [103], GST3 exhibited an upregulation pattern after 2,4-D treatment and the expression level of GST3 was not significantly different between resistant and susceptible corn poppy plants either 5 or 24 h after treatment, even though an upregulation of GST3 was stronger in the resistant plants. This result confirms that the expression of GST3 is induced by auxinic herbicides and that increased expression of GST3 is not involved in resistance to 2,4-D. Scarabel et al. [103] propose glyceraldehyde-3-phosphate dehydrogenase, actin and ubiquitin as the most stable reference genes for reliable measurement of gene expression levels during an NTSR study.

#### *Fitness Costs of Herbicide-Resistant Corn Poppy*

Some authors have also focused on the fitness costs of the poppy resistant biotypes. Fitness costs refer to several adaptations of herbicide-resistant biotypes—genetic, metabolic, growth-related and ecological—that the plant undergoes to survive in the herbicide-created environment [104]. In the tribenuron-resistant poppy biotypes originating from Greece in Thessaloniki and Serres, the fitness costs related to a mean growth rate (MGR) were 1.3 to 4.3 times lower than the respective susceptible populations, originating from sites within close proximity of their respective resistant populations. The resistant populations in Kilikis had similar or higher MGR values than the respective susceptible populations. The populations with the highest RI (above 2400) had low MGR values, and the populations with RI ranging from 1437 to 2227 had high MGR values. Other characteristics, such as fresh weight accumulation, seed production and capsule number of the resistant populations grown under field conditions, were similar to those recorded for the susceptible populations [88]. Another study examined early biochemical differences in the photosynthetic efficiency of photosystem apparatus (a light phase of photosynthesis) between biotypes of poppy susceptible and resistant to sulfonylurea herbicides, namely florasulam, metsulfuron-methyl and tribenuron-methyl [105]. It turned out that three days after herbicide spraying, the TSR population of poppy exhibited the maximum quantum efficiency of photosystem II (Fv/Fm) values similar to the untreated control, and these were about 20% higher than those of the sensitive plants in all herbicide treatments. This characteristic could provide the basis for early in-field detection of TSR poppy [105].

### **5. Characteristics of Herbicide-Resistant Cornflower in Poland**

The weedicology.org database contains just two research results for HR cornflower (*Centaurea cyanus* L.), both from Poland [13].

The potentially resistant seed samples were collected from arable fields in Warmia-Mazury Province (northeast Poland) in Paluzy, Równina Górna and Maruty, in 2009–2010, and then, dose-response tests were performed (Table 4). The tests revealed cross-resistance patterns to herbicides from the group of ALS inhibitors and chemical families in the studied biotypes: sulfonylurea (tribenuron, chlorsulfuron, sulfometuron) and imidazolinone (imazapyr) [106,107]. Furthermore, Marczevska and Rola [108] identified a chlorsulfuron-resistant cornflower (a single resistance) in fields of winter wheat

in southwest Poland in the village of Laskowice (Table 4). They carried out a dose-response test with the assessment of fresh and dry mass reduction in the resistant biotype following treatments with chlorsulfuron in doses from 0.5 to 32 times the field dose. As a result, they found that the resistant biotype was able to survive treatments even at the highest dose of chlorsulfuron, but fresh and dry shoot biomass decreased by 60% and 62%, respectively. Based on the results provided in the paper [107], the ED50 dose of chlorsulfuron, calculated for the resistant biotype, was equal to 254.25 g ha<sup>-1</sup> (11.3 times the field dose). In field trials, the Laskowice/2001 biotype proved to be sensitive to the mixtures of 2,4-D + fluroxypyr, 2,4-D + florasulam, 2,4-D + metosulam, isoproturon + diflufenican, MCPA + dicamba + mecoprop, chlorotoluron, and clopyralid [108].

**Table 4.** Characteristics of herbicide-resistant biotypes of *Centaurea cyanus* (L.) in Poland.

Biotype	Herbicide	HRAC <sup>1</sup> Group	RI <sup>2</sup>	Test <sup>3</sup>	TSR/NTSR <sup>4</sup>	Ref.
2/2009 1/2009 3/2010 4/2010	tribenuron, chlorsulfuron, sulfometuron, imazapyr	B/2; B	10.4; –; 4.6; 6.9 8.6; 7.1; 3.5; 4.2 8.2; 6.7; 1.1; 1.2 7.6; –; 3.3; 1.1	DRT	n/a	[106,107]
Laskowice /2001	chlorsulfuron	B/2	n/a, reduction in a dry mass of plants by ca. 60%	DRT	n/a	[108]

<sup>1</sup> HRAC – Herbicide Resistance Action Committee; <sup>2</sup> RI—resistance index; <sup>3</sup> DRT—dose-response test;

<sup>4</sup> TSR/NTSR—target site/non-target site resistance.

The biochemical and physiological state of ALS-cross-resistant cornflower biotypes 3/2010 and 4/2010 collected by Adamczewski and Kierzek [108] and exposed to tribenuron-methyl was tested by Saja et al. [109]. The authors found significant differences between the susceptible biotypes and the two resistant biotypes observed in dry seeds, seedlings and leaves both before and after application of the herbicide. The resistant biotypes were characterised by a higher germination capacity than the susceptible biotype. Moreover, significant differences were depicted in changes in the chemical composition of cotyledons, mainly a significant increase in the carotenoid and flavonoid content in the resistant biotypes compared with the susceptible biotype. The authors speculate that resistance to ALS-herbicides is probably also associated with the ability to acclimatise the photosynthetic apparatus to operate in the stress conditions imposed by the herbicide [109].

Marczewska-Kolasa and Rola [110] tested the biochemical changes of free amino acids in tissues of the resistant biotype collected in 2001 [108]. Based on the HPLC analysis, they found that in the aboveground parts of the resistant biotype treated with the recommended field dose of chlorsulfuron, the content of branched-chain amino acids, namely valine, leucine and isoleucine, increased significantly (by ca. 50%) in comparison with the herbicide-treated susceptible biotype. The authors conclude that target site resistance could be involved [110] as the synthesis of valine, leucine and isoleucine is catalysed by the acetolactate synthase, a target enzyme for the HRAC B-group of herbicides [111]. Additionally, the resistant biotype Laskowice/2001 treated with chlorsulfuron showed an increased heat emission two hours after herbicide treatment, measured by isothermal calorimetry, compared with the same biotype not treated with the herbicide [112]. The observed increase in a total heat flow from the tissues of HR biotypes was also observed for the other weed species, *Avena fatua* (L.) [113] and *Lolium rigidum* (Gaudin) [114], both of which are resistant to fenoxaprop-P (HRAC A).

## 6. Management of Resistant Corn Poppy and Cornflower

Although the frequency status of corn poppy and cornflower in Europe's segetal flora differs, i.e., poppy is a dominant weed, while cornflower is a rare one, management of resistant populations of both species should be treated as a priority due to the competitive pressure they place on crops but also on the biodiversity of segetal communities.

Only a few publications deal directly with the management of HR corn poppy, while there are no reports about HR cornflower control. This section therefore highlights the publications in which a



particular emphasis has been placed on the management of corn poppy or cornflower, irrespective of their levels of resistance to herbicides.

In accordance with the provisions of Article 14 of Directive 2009/128/EC and EC Regulation 1107/2009, since 1 January 2014, farmers in the European Union have been obliged to use integrated weed management (IWM) techniques to control weeds. This means that chemical control of weeds is allowed when the weed infestation exceeds the so-called economic threshold [115,116]. Monitoring fields to scout for weeds is the first step in making a decision about their control. In Poland, for cornflower infesting winter wheat on brown soil, the threshold is five plants  $\text{m}^{-2}$  [117], while for corn poppy, it is 6–10 plants  $\text{m}^{-2}$  [46]. Marshall et al. [118] indicate similar thresholds for corn poppy; the presence of 12.5 corn poppy plants  $\text{m}^{-2}$  results in a 5% reduction in winter wheat yield. Here, it should be emphasised that in the case of the occurrence of HR weeds in the field, they should be eradicated, irrespective of their threshold level. In order for IWM treatments to be effective, it is crucial to recognise the biology of biotypes present in the field. Dispersal of seed germination in time as well as the persistence of seeds in the soil play a key role in weed population dynamics, the establishment of weed communities and their successful control [2,33,119–121]. The timing of emergence affects plant growth, fertility, dormancy of the seeds produced and prospective dynamics of germination [34]. Poppy and cornflower emerge both in autumn and spring, and their emergences are lengthy, which makes both weeds difficult to control [34,36,122]. In winter cereals, corn poppy emerges between September and April, with the highest intensity in countries with a Mediterranean climate from September to December. According to Torra and Recasens [34], plants from earlier cohorts emerging between October and January are more fertile than those from later cohorts (February–April). Studies have shown that for populations resistant and sensitive to ALS inhibitors in the semi-arid conditions of Spain, both the emergence and peak of emergence were extended in time, but without differences between populations. The main emergence peaks of poppy were registered in autumn, with between 65.7% and 98.5% of the annual emergence taking place between October and December and only a limited emergence recorded in spring [17]. Moreover, nitrogen fertilisation may also promote a higher germination of poppy seeds, especially during the autumn [123]. Cohorts emerging immediately after crop sowing represent the main source of recruitment for the autumn weed population. The dormant seeds produced in autumn will be the main contributors to the soil seed bank and weed populations in subsequent seasons. All these recognised properties of corn poppy emergence can be used to plan its mechanical control. However, as the results show, this approach takes energy and time. Mechanical methods of corn poppy control should aim to promote emergence throughout the autumn and winter so that emerged seedlings can be controlled before a spring crop is sown by trying to deplete the soil seed bank as much as possible. As has been shown by Lutman et al. [33], in winter or spring wheat, systematic ploughing up to a 20 cm depth or cultivating with a flexible tine up to 10–15 cm over a six-year period caused a mean annual decline in poppy emergence rate of 9%, and an estimated emergence decline of 95% in 17 to 50+ years. The mechanical cultivation in winter wheat or spring barley performed over a five-year period showed a 40% decline in poppy emergence [124]. In conditions in which a high number of poppy seeds had accumulated in the surface soil following ten years of minimal cultivation, ploughing reduced seedling emergence by 40%. This effect was still evident for the next two years, but a second ploughing brought up the buried seeds, and the seedling numbers increased again [36]. The authors also noted that in dry years, the emergence rate of corn poppy was smaller, which can define a cultural management strategy for reducing its infestation and contribute to IWM strategies combining it with other tools [17]. Other research showed that the management outputs of HR corn poppy populations under different tillage systems, such as direct drilling, reduced or intensive tillage, crop rotation and delayed sowing combined with robust herbicide programmes, are similar. Therefore, less cost-intensive no-till methods should be further elaborated for successful control of HR poppy [125]. Another example of a no-till cropping system was tested by Luna et al. [126], who used what is known as ‘pasture cropping’, where annual crops are sown into living perennial pastures during their dormant stage. In this type of cropping, when

barley was sown between two perennial summer species, *Cynodon dactylon* (L.) and *Eragrostis curvula* (Schrad.), a significant decrease in corn poppy density of around 55–96% was noted in a mixture of barley + *C. dactylon* [126].

With regard to cornflower, the influence of tillage on its occurrence has also been confirmed, but the results contrast with those for corn poppy. Numerous authors point to a greater frequency of cornflower in a crop following reduced tillage by rototiller and disc performed continuously for a few seasons [127,128]. This effect is evident, for example, after four years of reduced tillage in winter oilseed rape [129]. The number of weeds in arable fields is also determined by the sowing date of the crop. According to studies by Hanzlik and Gerowitt [66] and Tyburski et al. [130], one effective way to reduce the number of cornflower plants is to delay the sowing date of winter wheat and winter rapeseed, leaving more time for mechanical control of this weed.

For effective chemical control of a resistant biotype, herbicides of different mechanisms of action should be applied, preferably those used as mixtures. The effectiveness of this approach has been emphasised in many publications. For ALS-resistant biotypes of poppy, the recommended herbicides include HRAC K1 (dinitroanilines, i.e., pendimethalin) or/and HRAC C2 (urea derivatives, i.e., chlorotoluron) [80], HRAC O (phoxycarboxylic acids, i.e., MCPA) or/and HRAC C3 (nitrile, i.e., ioxynil + bromoxynil) [9], HRAC O (phoxycarboxylic acids, i.e., 2,4-D) or HRAC C3 (nitrile, i.e., bromoxynil) in a mixture with sulphonamides (i.e., metosulam HRAC B) [83]. For the chlorsulfuron-resistant biotypes of cornflower, usage is advised of herbicides from the group HRAC C2 (urea derivatives, i.e., chlorotoluron) or HRAC O (phoxycarboxylic acids, i.e., MCPA + 2,4-D and pyridinecarboxylic acid derivatives, i.e., fluroxypyr or chloropyralid) [108].

Combining a method of mechanical control with chemical control is practised in the control of HR weeds. This approach has been verified in conditions in northeastern Spain by Recasens et al. [131], who tested four farming practices in three-year long field experiments under no-till, with the aim of reducing the density of a multiple HR corn poppy population. The applied combinations included: (1) traditional, where winter barley was sown in a three-year monoculture with chemical weed control only, (2) winter cereal rotation, wheat–barley–wheat, with delayed-sown barley and chemical weed control, (3) crop rotation, pea–winter barley–winter wheat, with delayed-sown barley and rotation of herbicides of different sites of action, and (4) low-input, winter barley–fallow–winter barley, with delayed-sown barley at high density and weeds controlled mechanically by flexible rod harrow in cereal and by shredding in fallow. The herbicides applied in the study included pre-sowing glyphosate (HRAC G) and mixtures of bromoxyl (HRAC C3) + MCPA (HRAC O), aminopyralid (HRAC O) + florasulam (HRAC B), pendimethalin (HRAC K1) + imazamox (HRAC B), chlortoluron (HRAC C2) + diflufenican (HRAC F1), and isoxaben (HRAC F2), applied differently in different years and for selected combinations. As a result, after three years of the experiment, HR poppy densities were reduced by between 35% and 76–93% for the low input and all the other combinations, respectively. The authors conclude that farmers need to find a balance between crop profitability under no-till and minimising their carbon footprint while controlling a herbicide-resistant population. In this scenario, the short-term priority should be to reduce the presence of multiple HR biotypes, integrating the different chemical, cultural and physical strategies available [131].

Furthermore, the allelopathic potential of crops could be used to reduce the number of weeds, especially by increased crop density and the use of older, more competitive varieties [132,133]. This approach has been studied by Dhima et al. [134], who observed that under field conditions, a reduction in corn poppy fresh mass by about 10–90% could be achieved when some old barley cultivars were grown and competed with the poppy.

Recently, there has been a trend in developing combine harvesters and other machinery that exploit the potential to destroy weed seeds during harvest [135]. One of the options is to construct combine harvesters that use exhaust gas to either kill or reduce the ability of weed seeds to germinate before the seeds are returned to the field. As research has shown, exposure of 140 °C for four and six seconds repressed the germination of cornflower seeds [136,137], whereas exposing chaff with

cornflower seeds to 150 °C for 10 s deprived the seeds of germination [138]. Possibilities of using this finding in commercial combine harvesters were proposed [139]. The other solution, also dedicated to destroying HR weed seeds during harvest, is a Harrington seed destructor, which is also a potential way of destroying cornflower seeds [138] as they often land in the harvested grains [140]. The idea of this destructor is to mill the weed seeds along with chaff processing, using a specially developed cage [141].

## 7. Conclusions

The research results highlight many reasons for the decrease in cornflower frequencies on Europe's arable land. The self-incompatibility of this species and lack of active pollinators has led to a reduced seed set, resulting in a loss of genetic diversity and a weakening of the population. An additional factor significantly accelerating the disappearance of cornflowers from fields appears to be agricultural intensification, including an increased level of fertilisation and application of herbicides. In contrast, the great adaptability of corn poppy to different environmental conditions, resulting from its wide genetic plasticity, could promote the rapid development of herbicide-resistant biotypes under the selective pressure of herbicides. Poppy biotypes resistant to ALS inhibitors and phenoxy-carboxylic acids are a particular threat to cereal crops in southern Europe (Greece, Italy and Spain), and in the north (Great Britain). In central and eastern Europe, HR biotypes of poppy are much less frequent. However, it should be emphasised that biotypes of poppy resistant to C1 herbicides have only been found in Poland and HR cornflower has so far only been recorded in Poland. However, even a species with a low risk of evolving resistance can become a problem, as highlighted by Moss et al. [17], and cornflower is one such example of this.

TSR to ALS inhibitors in corn poppy has been well studied, with mutations found in codons 197 and 574 of the ALS gene. Poppy biotypes with NTSR to ALS inhibitors and growth regulators have also been reported. The importance of NTSR to ALS inhibitors may well be underestimated in broadleaved weeds, possibly because it is very often associated with TSR. There are no reports in the literature of the molecular basis of cornflower herbicide resistance. Based on the biochemical analysis of one of the ALS-resistant biotypes, it can be concluded that TSR was involved in this biotype. Nonetheless, this phenomenon merits further study.

Presently, there are 25 active ingredients registered for the control of corn poppy and cornflower in the EU. The EU market of herbicides for controlling corn poppy and cornflower is dominated by herbicides from the HRAC B and HRAC O groups. These a.i. are classified as having a high (HRAC B) or medium (HRAC O) risk of developing resistance. Research to date indicates that it is possible to control resistant poppy biotypes by using herbicides with other sites of action, especially mixtures of them. A greater exploration of the competitive and allelopathic potential of crops against HR biotypes of corn poppy and cornflower could be of interest. It would therefore be worthwhile to undertake comprehensive research in various soil and climatic conditions to explore the mutual competitive abilities between crop, HR biotype and other herbicide-susceptible species of weeds. More accurate studies on the fitness of biotypes of both HR weeds as well as studies of genetic diversity within biotypes could help with their effective control. At the present stage of knowledge, there is a lack of information on the extent to which HR biotypes of corn poppy or cornflower affect crop yield.

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