A review of broad-leaved weed resistance 2006- 2007

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Summary

The current status of herbicide-resistance in broad-leaved weeds world-wide has been reviewed and summarised in order to help predict which species are likely to evolve resistance in the UK. Herbicide resistance continues to challenge agriculture and horticulture, and is a potential threat to the industrial and amenity sectors. This review uniquely investigates the problem of herbicide resistance from the chemical and biological point of view. In the UK populations of herbicide resistant common chickweed (*Stellaria media*) and common poppy (*Papaver rhoeas*) have been identified and have therefore been selected as key species for this review, including details of population biology, 'weediness' and agroecology. Canadian fleabane (*Conyza canadensis*) is an increasing problem in the amenity sector and has therefore also been included in more detail. The Amaranth family (*Amaranthus spp*.) were included due to their importance globally and to identify and lessons. In summary the most important biological factors that could potentially contribute to the resistance risk include high seed production, the 'weediness' of a species, more than one generation per season and the presence of resistance already in a similar system. Taxonomy appears to not be relevant when predicting resistance risk in a weed species and type of pollination method was inconclusive. The most important chemical factors include herbicide mode of action, mode of use (ie. alone or mixtures and sequences, or multiple applications in a season), intrinsic activity and residual activity. Cultural control continues to have a major role to play in herbicide resistance management strategies.

Background

The number of reported cases of herbicide-resistant weeds, which globally continue to increase each year, now stands at 315 biotypes (Heap, 2007). From the mid 1970s resistance to triazines had the highest number of weed biotypes, however through the late 1980s and early 90s changes in herbicide use and new chemistry led to a rapid increase in ALS-inhibitor resistance, and this is now the largest group (Tranel & Wright, 2002; Heap, 2007). Since 2000 there has also been a sharp increase in glyphosate resistance in the USA, which could be attributed to the introduction of Roundup Ready crops and poor crop management strategies.

In a survey by Moss (2004) involving respondents in 12 countries, herbicide-resistant common poppy (*Papaver rhoeas*) was rated the third most important herbicide-resistant weed in Europe, after black-grass and rye-grass. Within the UK ALS-resistant poppy has been identified in 7 counties of England and ALS-resistant chickweed (*Stellaria media*) in 6 counties of Scotland and 5 counties of England.

Some preliminary cross-resistance studies with chickweed indicated that the degree of resistance might vary with population and cross-resistance might extend to herbicides with different modes of action, such as fluroxypyr and mecoprop.

Because herbicides with new modes of action are not being developed there is over reliance on fewer existing products, many of which are high risk resistance groups; for example ALS inhibitors (Tranel & Wright, 2002). Where resistance occurs, growers face costly control (often involving increased cultural control), and major inconvenience. It is therefore difficult for growers to balance long-term planning strategies and short-term financial constraints.

Objective

The overall objective was to review the current status of herbicide-resistance in broad-leaved weeds world-wide in relation to their population biology, 'weediness' and response to different herbicides, in order to help predict which species are likely to evolve resistance in the UK agriculture, horticulture, industrial, and amenity sectors. The first specific objective included identifying the risk of an individual weed species' propensity to evolve resistance (comparing those that have already evolved resistance to those that have not), related to their population biology, agroecology and 'weediness'. The second specific objective involves identifying the risk imposed by different herbicides. For both the biology and herbicide sections of the review particular emphasis will be on Europe and the UK.

Structure of the review

This review is divided into four sections. In the first section a background review covers the history of the development of herbicide resistance in those parts of the world where herbicides are used, and reviews the biology of the two most prominent broad-leaved weed species in Britain where herbicide resistance has been observed. This section also includes information on the risks posed by specific herbicide and cultural factors. The second section uses statistical methods to appraise the risk factors associated with certain biological traits common to weeds, which may be associated with the development of herbicide resistance. The final sections draw together the information presented above and summarises the risks.

1. History of herbicide resistance

1.1 World-wide status of herbicide-resistant broad-leaved weeds

Many papers and reviews have been written over the last 15 years highlighting the problems of resistant weeds worldwide. For example Moss and Rubin (1993) published a concise review covering many aspects of herbicide resistance from the early 1980s, which covered the incidence, development, selection pressure and fitness of resistant weed species, in relation to resistance mechanisms and prevention and control of resistance. They concluded that more research was required to better understand the complex interaction between weed ecology, herbicide mode of actions and the genetics and mechanisms of resistance and that integrated approaches combining chemical and cultural methods were required for managing herbicide-resistance. By the late 1990s the latest findings from the 'International Survey of Herbicide-Resistant weeds' (ISHRW) originally collated in 1995/96 (sent to 53 countries) that monitors the evolution of resistant weeds worldwide and assesses their impact, were presented by Heap (1997 and 1999). The survey showed that by 1997 there was a relatively constant increase in new cases of herbicide-resistant weeds being recorded (approximately nine new cases a year world-wide). When surveying began in the 1970's by LeBaron and Gressel (LeBaron, 1991), on average only one new species was recorded as resistant per year (between 1970 and 1977). Between 1978 and 1983 weed scientists recorded 33 new cases of triazine-resistance (making up 67% of all recorded resistant weed species), due to the widespread use of simazine in orchards and atrazine in maize. As herbicides with new modes of action were introduced to the market through the rest of the 1980's and 1990's there was a shift in herbicide-resistance from predominately triazine-resistance to these alternative modes of action (Figure 1).

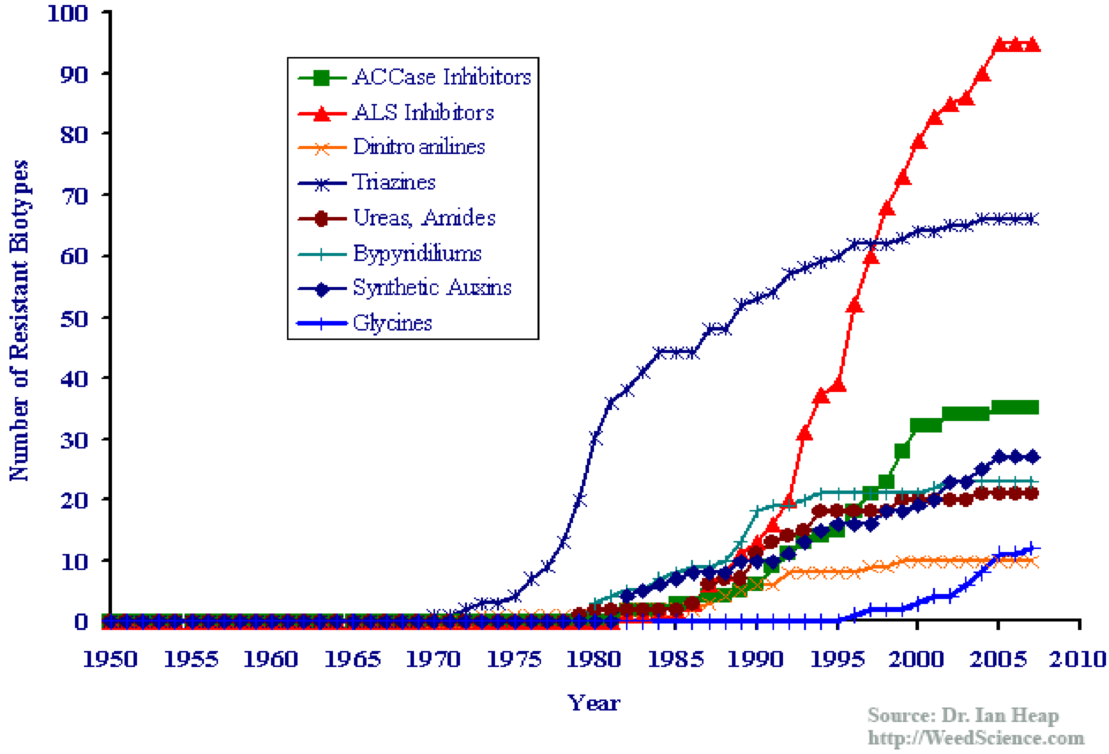

Figure 1. The number of resistant biotypes of weed species recorded via the International Survey of Herbicide-Resistant weeds up to 2007.

The findings of the ISHRW are available on the Weed Science website (www.weedscience.org). The information shows that by 2000, the three herbicide classes with the greatest number of resistant biotypes were the ALS inhibitors, the triazines and the ACCase inhibitors in that order and this remains the same in 2007. What is striking is that since the introduction of the ALS inhibitors in the early 1980s, the number of ALS resistant biotypes has increased dramatically and has now overtaken the triazines – first introduced around 25 years earlier. Although the ACCase inhibitors are third in terms of number of resistant biotypes, they are used solely against grass-weeds, in contrast to the triazines and ALS inhibitors, which are used against both grass-weeds and broad-leaved weeds. ACCase inhibitors were first used extensively from the mid 1970s, and consequently resistance has evolved relatively rapidly, especially when one considers that the majority of weeds worldwide are broad-leaved weeds, not grasses.

Resistance does occur to many other herbicide classes, but some of these have been used for much longer periods than the ALS and ACCase inhibitors. For example the synthetic auxins (e.g. MCPA, 2,4-D) have been used widely since the mid 1950s for broad-leaved weed control, and the dinitroanilines (e.g. trifluralin) and the bypyridiliums (e.g. paraquat) since the 1960s against grass and broad-leaved weeds. Yet despite this longer period of use, far fewer weed biotypes have evolved resistance to these herbicide classes.

Resistance to ALS-inhibiting herbicides has evolved in many countries, especially North America, Australia, Japan, and to a lesser extent South

America and Europe (Figure 2). In America, populations of chickweed developed resistance to the sulfonylurea herbicides after five years of continuous use of these chemicals in wheat crops (Reed *et al*., 1989).

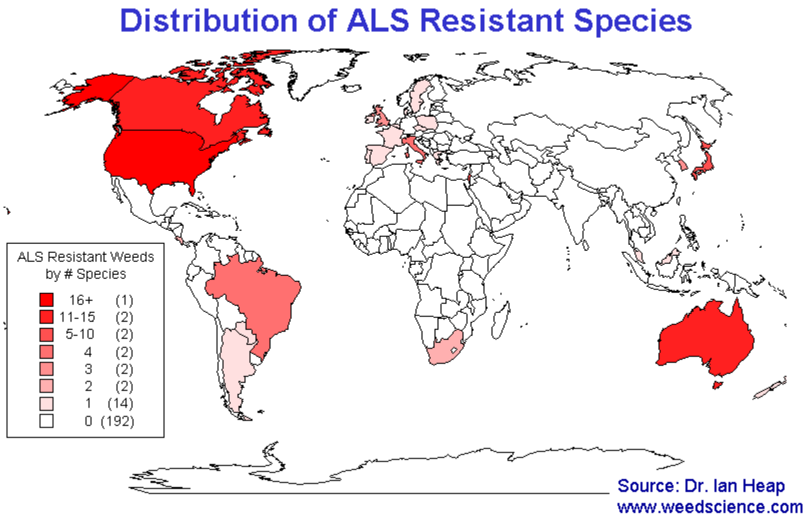

Figure 2. The distribution of ALS-resistant weed species worldwide, as collated by Heap 2007.

In total 315 resistant weed biotypes have been identified worldwide, representing 183 different species (110 dicots and 73 monocots). Of these species 95 ALS-resistant and 35 ACCase-resistant biotypes have now been identified (Heap, 2007). The resistant weeds were summarised into families by Holm *et al*., (1997) and have been updated to 2006 (Table 1), listing the top ten main families. As so many different families are represented could indicate that there is no clear pattern or trend with family grouping.

Table 1. The top ten weed families World-wide from a total of 29 families containing 182 resistant weed species by 2006. (*Updated from original table in Holm 1997 with data from Heap, 2007*).

Weed Family	**No. Species/family**	**% Resistance of total**	**Worst Weeds %[a]**
Poaceae	60	33	25
Asteraceae	32	18	16
Brassicaceae	14	8	4
Amaranthaceae	11	6	3
Chenopodiaceae	8	4	2
Scrophulariaceae	7	4	1
Polygonaceae	6	3	5
Alismataceae	5	3	1
Cyperaceae	4	2	5
Lythraceae	4	2	1
Solanaceae	4	2	2
Others (pooled)	27	15	16
Totals	182	100	81

[a] *The number of species within a family (as a percentage of total) reported by Holm et al., (1991 & 1997) as being principle weeds of the world.*

The herbicide groups from which a number of different weeds have developed resistance are listed in Table 2, with the number of biotypes recorded in 1997 and then ten years later in 2007. The three herbicide groups that have seen the biggest change in the number of resistant biotypes recorded in that period are the ALS-inhibitors, synthetic auxins and glycines (Table 2).

Table 2. Number of herbicide resistant cases listed by herbicide group from Heap (1997) updated from Heap (2007) ISHRW website. The species with the most increase over the ten-year period are highlighted.

Herbicide group	Example herbicide	No. of resistant broad-leaved weeds	
		1997	**2007**
Triazines	Atrazine	43	**49**
ALS inhibitors	Chlorsulfuron	26	**71**
Bipyridiliums	Paraquat	15	**16**
Ureas/auxins	Chlorotoluron	5	**8**
Synthetic auxins	2,4-D	12	**20**
ACCase inhibitors	Diclofop-methyl	0	**0**
Dinitroanilines	Trifluralin	1	**2**
Triazoles	Amitrole	1	**1**
Nitriles	Bromoxynil	1	**1**
Glycines	Glyphosate	0	**8**
Thiocarbamates	Triallate	0	**0**

1.2 Broad-leaved weed resistance in the UK

Within the UK there are 11 broad-leaved weed species that have been recorded with herbicide resistant biotypes. However, of these, 7 are resistant to the triazine group of herbicides and are located predominately in orchards or hops growing areas of the south east of England, where simazine was routinely used in the 1970s and 80s. For the purpose of this review triazine-resistance will not be covered, therefore main weed species that will be focused on are common poppy and common chickweed, of which populations resistant to ALS-inhibiting herbicides have been studied. In the UK herbicide resistance in common poppy was first detected in 2001, on 11 farms within 7 counties in England. Resistance in chickweed was first detected in 2000 and was reported on 15 farms, within five counties in England and six counties in Scotland (Moss *et al*., 2005). Other species that have been considered include Canadian fleabane (*Conyza Canadensis*) which is becoming a more common weed of horticultural and field crops in Britain and the Amaranth family (*Amaranthus* spp.), which is not currently a problem in the UK but an extremely important global issue, therefore both of these additional species will be discussed in greater detail.

1.3 Weed biology

1.3.1 Common Poppy (Papaver rhoeas)

Common Poppy (belonging to the Papaveraceae family) is a very competitive and abundant annual weed in the UK. It is distributed all over the world, but is most frequently found in Europe where it originated. Common poppy can be found in all arable crops (predominately winter cereals), gardens, meadows, roadside verges and disturbed land or waste sites. In the UK common poppy is predominately found in England and SE Scotland and is less common in Wales and the rest of Scotland. It favours a soil pH of 6.0 to 8.0 (Grime *et al*., 1988). There are five annual *Papaver* species found in the UK, the most common being *P. rhoeas*, but *P. dubium* L. (Long-headed poppy) is also widespread and the two species are frequently found together in cultivated fields or waste land (McNaughton & Harper, 1960). The other three species are *P. argemone* L. (Prickly poppy), *P. lecoqii* Lamotte (Babington's poppy) and *P. hybridum* L. (Rough poppy) which are all less common and localised.

Lifecycle and Seed production

Common poppy requires cross-pollination, as individual plants are completely self-incompatible and are normally pollinated by insects, predominately the honey bee and the bumble-bee (McNaughton & Harper 1960). They flower between June and October, with the main flush in June and July. A further flush of flowers may occur after crop harvest (Grime *et al*., 1988). Common poppy is very competitive in an arable wheat crop and will produce a range of numbers of pods per plant depending on the plant density and competition. For example at a plant density of 270 plants/m^2, six capsules per plant were recorded (Holm, 1977) however at higher plant densities only one capsule per plant is common. Generally this species produces a very high number of seeds per capsule. Hanf (1983) quotes approximately 20,000 seeds per plant, but a recent review by Bond *et al*., (2006) refers to between 10,000 to 60,000 seeds per plant.

Germination and emergence

The main germination period for common poppy is most commonly considered as the autumn (Hanf, 1983). However Roberts & Boddrell (1983) studied the seedling emergence patterns of four species of poppy and reported from their experiments that emergence of common poppy was greatest in the spring. Poppy seeds require light to germinate, so they emerge at a very shallow depth. Common poppy seed has a morphophysiological dormancy when initially shed (Baskin *et al*., 2002) and requires at least 12 weeks in the soil with alternating temperatures and moisture before germination occurs.

Seed persistence

Common poppy seeds can survive for a very long time in the soil seed bank (Chancellor 1986), with an average annual decline rate of only 6.2%. This is very similar to the findings of Lutman *et al*., (2002) who reported an average seed decline rate of 9% per year.

Competition, growth and genetic variation
Common poppy can be a highly competitive weed in a cereal crop as seedlings often emerge at the same time as the crop, competing for light and nutrients. In a poorly established crop common poppy can produce a high plant biomass and depress the crop yield (Wright *et al*., 1997). The density of the crop and the presence of other weeds will affect the seed production ability of the poppy. The occasional hybrid of Common poppy (*Papaver rhoeas*) and Long-headed poppy (*P. dubium* L.) has been recorded (McNaughton & Harper 1960), but these are much less vigorous and rarely survive. The question of why these two species rarely hybridise, although commonly being found together, could be explained due to the fact that Long-headed poppy has the ability to set-seed from self-pollination, while common poppy does not. In addition the honey-bee, which is the main insect pollinator, is able to distinguish between the two species, thus providing a partial barrier to cross pollination.

1.3.2 Common chickweed (Stellaria media L. (Vill.))
Common chickweed is a member of the Caryophyllaceae family and is one of the most widely distributed annual weeds (occasionally perennial) globally (Holm, 1977). It is found all over the UK in cereal fields, oilseed rape, sugar beet and is predominant on field margins. As part of the Countryside 2000 survey chickweed was recorded as one of the most frequent broadleaved weed species in cereal field margins in the UK (Firbank *et al*., 2000).

Lifecycle and seed production
Chickweed is self-pollinating and its great success appears to be due to its ability to colonise an area quickly, as seeds are not adapted for long distance dispersal. Although this species is predominantly self-pollinating there is a short period of time where insects can cross-pollinate the plants (Grime *et al*., 1988). Despite being a self-fertilising species the success of chickweed as a vigorous weed can be attributed to its extremely diverse and variable forms (Salisbury, 1974).

Chickweed can flower and set seed very rapidly (a complete lifecycle can be as short as 5-6 weeks) and flowering can last over a very long period of time in temperate zones producing very high numbers of seed. Chickweed can flower every month of the year, but generally flowers from early spring to late autumn in the UK (Grime *et al*., 1988), however each flower only lasts for one day. A seed capsule on average contains 6-10 seeds, but can contain between 1 and 20 seeds. The average number of seeds per plant will vary depending on the location of the plant, its size, and the amount of surrounding competition. Salisbury (1974) reported an average number seeds per plant as 2,400, while Hanf (1983) quotes an average seed production of 15,000 seeds. Lutman (2002) studied the relationship between plant dry weight (g) and seed production per plant and the studies included chickweed growing alone and in 3 spring crops, spring field beans, linseed and spring wheat. It was concluded that there was a strong correlation between $\log_{10}$ plant weight and $\log_{10}$ flower number (R^2=0.89) and from these data it was calculated that a plant dry weight of 1g would produce approximately 80 seeds per plant, while a dry weight of 100g produced 13,100 seeds per plant.

Germination and emergence

Chickweed seeds can germinate readily, showing very low levels of dormancy and tolerate a wide range of soil types and very cold temperatures, preferring cool, moist shady places (Holm *et al.,* 1977). Both temperature and water potential affect the germination of chickweed (Grundy, 1997), although the relationship can be complex, determined by seed age and population. There are two main flushes of germination, one in the autumn and the second in the spring. Christal *et al*., (1997) investigated 25 different chickweed populations collected from across the whole of the UK to determine any inter-population variation and concluded that there were significant differences in germination and seedling growth between the populations tested, which were a result of genetic variation within the species. A wider study across Europe and the USA (Grundy *et al*., 2003) also highlighted the variability in germination and emergence of different chickweed populations and how local climatic conditions affect emergence behaviour.

Seed persistence

There is a lot of variation in the literature concerning the seed persistence of weed species. Cultivation, soil type, crop rotation and competition all play a role in determining the fate of seeds in the soil. Seed predation and mortality are also important factors that are quite often ignored or excluded from estimations of seed return to the soil. Salisbury (1974) reported that chickweed seeds retain viability for 25 years. Chancellor (1986) calculated an average seed decline rate of 26.2% per year for chickweed seed that had been buried under grass (previously arable land) for 20 years. It has more recently been reported that this species has an average annual decline rate of 35% and an estimated time of 7-8 years to reach 98% decline (Lutman *et al*., 2002). These experiments were carried out over a 6 year period and included cultivations and a spring and winter sown crop on two soil types. Similarly, Lawson & Wright (1993) concluded that it would take an average of 11.1 years to achieve a 99% reduction in seeds. Seed persistence of chickweed is summarised in a review by Bond *et al*., (2006), which clearly highlights the variation in published data, ranging from a seed longevity value of 2.5 years in dry storage at low temperatures to 60 years under grass.

Competition, growth and genetic variation

Chickweed can be out competed, as it needs space to thrive. As a consequence it has adapted well to cultivated land that is regularly disturbed. In a thick cereal crop chickweed plants would generally remain low to the ground and be small in size due to the competitive effect of the crop canopy limiting light. However, in a more open crop such as linseed or field beans chickweed plants tend to grow large in size, forming dense mats of plant material and a lot of seeds are produced per plant. Chickweed plants are sensitive to drought and it is one of the first weed species to wilt with a lack of water (Sobey, 1981).

Chickweed benefits from increased nitrogen levels in the soil, which explains why it is so common in intensive arable cropping systems. Molecular studies were carried out on chickweed collected from plots within the Rothamsted Broadbalk long-term wheat experiment that have received the same nitrogen applications for 150 years (Cavan *et al*., 2000). The results showed that distinct biotypes of chickweed have evolved on plots with different levels of nitrogen input. Where chickweed is present under low nitrogen treatments the genetic diversity is lower, which could be a result of intense selection in the past, due to the less favourable growing conditions.

1.3.3 Canadian fleabane (Conyza canadensis)

This weed is native to North America and is an annual, which can follow a summer or winter annual cycle. It is also known as Horseweed and marestail in America. It is predominately a problem weed in the States of Indiana, Ohio and Illinois. Canadian fleabane is however found in the UK and is reported to have increased since the early 1960s (Preston *et al*., 2002) and is now common in the majority of southern England and the Channel Islands. It is much less common in north and west England and rare in Scotland (Stace, 1997).

Lifecycle, seed production and persistence

Canadian fleabane is a self-pollinating weed and pollen is released before the capitulas are fully open. However, a small amount of out-crossing has been observed, but is very uncommon. This weed produces a large amount of seed (Loux *et al*., 2006), which is dispersed by wind due to a presence of a pappus, often resulting in rapid and vast spread of the seed across agricultural land. There have been a number of estimates of the number of seeds per plant (summarised by Bond *et al*., 2007) of between 25,000 and 200,000 seeds and approximately 80% of these seeds will germinate immediately after shedding. Weaver (2001) reported that viable seeds of Canadian fleabane were found in seed bank samples from a site that had been as pasture for 20 years.

Germination and emergence

Canadian fleabane seed germinates readily and quickly after shedding, either in the autumn or spring. In the Northern regions of the USA the plant remains as a basal rosette of leaves throughout the autumn and winter and then bolts in the spring (Loux *et al*., 2006), usually in April. Approximately 90% of plants that overwinter survive to become mature plants and flower and produce seed in about July. However, where this weed germinates in the spring it is one of the most troublesome spring emerging annual weeds, as the rosette stage of the plant growth is very short and bolting occurs very rapidly. In the UK Canadian fleabane typically flowers between June to October (Hanf, 1970).

Competition, growth and genetic variation

Canadian fleabane is a very competitive weed and can tolerate drought stress even when a crop is suffering due to lack of water. Due to the common cropping practice of non-tillage in some of the Southern states of America where this weed is very common it has become extremely difficult to control.

It has been reported that yields of soybean have been reduced by up to 83% as a result of competition with this weed in the USA (Bruce & Kells, 1990).

1.3.4 Amaranths (Amaranthus spp.)

The Amaranth *spp*. are summer annuals, common throughout the USA in agriculture, horticulture, roadside verges, nurseries and pastures. There are 12 different species of importance in the USA, with Palmer Amaranth (*Amaranthus palmeri*), Redroot pigweed (*A. retroflexus*) and Smooth pigweed (*A. hybridus*) being the most common. The biology of amaranths have been well described by Costea and Tardiff (2003 and 2004). All the amaranth species show a high degree of variability and some species such as *A. rudis* and *A. retroflexus* may hybridise. Redroot pigweed is often used as a green vegetable crop, cooked in a similar manner to spinach while the grains are used as a source of starch especially useful for coeliacs.

Lifecycle and seed production

Amaranth species germinate in summer temperatures and develop rapidly, coming to flower very quickly. Some species for example *A. rudis* contain either male or female flowers (dioecious) flowers and so are forced to outcross. Others such as smooth pigweed, *A. hybridus*, are monoecious and may have limited self-crossing (Appendix 2, Table 2). Flowering continues throughout the season. *A. albus* seeds mature rapidly within 20 to 30 days after flowering onset. *A. blitoides* develops so fast that there may be two generations within a season. Plant size seems to correlate with the number of seeds produced. Seed number varies between thousands and hundreds of thousands (Appendix 2, Table 2).. There are different rates of phenological development between species and these may be reflected in their different weedy characteristics in crops.

Germination and emergence

Steinmaus *et al.,* (2000) modelled the germination of several weed species to estimate the base temperature at which seeds would germinate. They estimated a difference of 1 degree between *A. albus (about 16°C)* and *A. palmeri (17°C).* Germination rates in these two species were high at up to 80%. Guo and Al-Khatib (2003) showed that *A. retroflexus* and *A. palmeri* germinated and developed best at high temperatures of 30 to 35°C whilst *A. rudis* had peak germination at 20 – 25°C. Germination in all weedy species is stimulated by light in near surface seeds, so that cultivation stimulates their emergence (Weaver 2001).

Seed persistence

There are little data on viability and longevity of amaranth seeds, but they are probably relatively persistent. Viability, germination and seed return vary with cultivation and ecology.

Competition, growth and genetic variation

Yield losses for several Amaranth species in several crops in the USA are shown in the Appendix Table 1. Plants that emerge at the same time as the crop can significantly reduce yield, while as the season progresses late emergers have less effect with reduced biomass and size. Nevertheless these weeds still have a significant seed shed (Hartzler *et al*., 2004). Sibony and Rubin (2003) found that ALS resistant *A. retroflexus* and *A. blitoides* were as fit, in terms of biomass, as the non-resistant biotypes, although triazine resistant types were less fit.

1.4 Herbicide modes of action and resistance risks

When herbicide resistance develops in a weed biotype, the key factor determining whether a widespread problem will occur is the rate at which resistance can build up. Many factors are involved, but the most important are likely to be the efficacy and frequency of use of the herbicides selecting for resistance and the population dynamics of the individual weed. One reason why grass-weeds are over-represented in occurrence in the herbicide resistance database maybe that they generally have the capacity for a more rapid population increase (often 10-fold per year or more) than most broad-leaved weeds.

Herbicide modes of action

There are a large number of different herbicide modes of action and these are categorised according to their specific biochemical activity. Examples include inhibitors of photosynthesis, lipid biosynthesis, amino acid biosynthesis, and cell division (Zimdahl, 1999). The main groups of herbicides associated with resistance in broad-leaved weed species are briefly described below.

1) ACCase inhibitors

The ACCase inhibiting herbicides (lipid biosynthesis inhibition) are used solely against grass weeds and therefore are not relevant for inclusion in this review of broad-leaved weed resistance. Grass weeds have a generally much lower seed persistence, therefore there is less buffering from old seed in the seed bank.

Potential UK resistance risk: <u>Negligible</u>

2) ALS inhibitors

The use of ALS-inhibiting herbicides (amino acid biosynthesis inhibition) has become very widespread globally since the introduction in the early 1980s, with chlorsulfuron for broad-leaved weed control in cereals. Today this herbicide group is currently responsible for the largest number of weed species that have selected for a particular resistance type (Tranel & Wright, 2002; Heap, 2004). They are a popular group of herbicides as they are used at very low rates, control a wide weed spectrum, show high levels of efficacy and have low toxicity to mammals (Heap, 1997; Zimdahl, 1999; Tranel & Wright, 2002; Scarabel *et al*., 2004). Within this group of herbicides the sulfonylureas are amongst the most widely used, often in successive years, leading to resistant weed species developing extremely quickly, in some cases after only 3 years of annual exposure. Resistance has been detected typically after an exposure time of between 4-6 years for the majority of sulfonylurea-resistant weeds in the USA where continuous use has occurred (Mallory-Smith *et al*., 1990). However in Denmark, sulfonylurea-resistant chickweed was identified after 7 to 8 years of continuous exposure (Kudsk *et al*., 1995). The relatively long time before resistance was detected in this case may have been due to different climatic conditions and soil pH along with the lower recommended rate of product use in Denmark. The imidazolinones have a slightly lower activity level to the sulfonylureas and generally high soil persistence levels that affects choice of crop rotation.

Sulfonylureas are often the sole herbicide used in some countries (USA & Australia) where yield potential is low (typically 2 t/ha) and therefore expenditure is restricted. However, the situation is very different in the UK & Europe, where potential yields are much higher (typically 8 t/ha) and the use of sulfonylureas as a single active ingredient is much more rare. This may be why resistance to ALS inhibitors has been less common in Europe than elsewhere, with chickweed as the first resistant weed recorded in Denmark in 1995 (Kudsk *et al*., 1995). There are indications however that this situation is changing – six of the nine new cases of resistance recorded in Europe during the last three years involve ALS inhibitors (Moss, 2004). Populations of ALS-resistant common poppy have been studied in Italy and it was concluded that resistance is due to point mutation in the ALS gene conferring amino acid substitution at the Pro-197 position of the ALS enzyme, and that resistance is inherited as a dominant monogenic trait (Scarabel *et al*., 2004). This was the first ALS target site mutation conferring resistance to have been completely characterised in common poppy, although other target site resistant populations have been detected since 2004. Since their introduction ALS inhibiting herbicides have mainly been targeted at broad-leaved weeds, and consequently resistance has developed in 72 broad-leaved weed species worldwide (Table 1, Appendix 1), an increase from 33 species in 1997 (Heap, 1997). Resistant weed species have been recorded in numerous different crops globally including cereals, soybean and rice and also non-cropped areas such as rights -of -way and forestry plantations.
Potential UK resistance risk: <u>Very High</u>

3) Phenylureas and phenylamides (eg. Chlorotoluron, IPU)
The phenylurea herbicides (photosystem II electron transport inhibitors) are broad-spectrum herbicides that are absorbed into the plant via the soil. They are most effective on small germinating seedlings, however will persist in the soil to give protracted control.

Broad-leaved weed species resistant to phenylureas include an Indian population of *Phalaris minor* Retz, resistant to isoproturon, which is of major economic concern as it threatens the wheat growing areas (Heap, 1997).

Chlorotoluron-resistance has mainly occurred in grass weed species, such as *Alopecurus myosuroides* and *Alopecurus japoniens*. Propanil-resistance (amide) in grassweeds *Echinochloa crus-galli* Beauv. and *E. colona* Link have been identified in north and south America and Greece. This group of herbicides are considered as low risk to broad-leaved weeds in the UK and Europe.
Potential UK resistance risk: <u>Low</u>

4) Bipyridiliums (eg. Paraquat and diquat)

These non-selective herbicides (photosynthesis inhibitors) have been widely used across the world for weed control (predominately in orchards and plantations) since their release in the late 1950's (Heap, 1997). They are very popular products due to their fast acting post-emergence action and non-persistence. They act solely through foliage absorption and are not translocated within the plant therefore needing complete contact and will not move into plant roots. Paraquat is most effective on grass weeds and diquat on broad-leaved weeds and are both commonly used for pre-harvest desiccation of crops (Zimdahl, 1999). However, paraquat is being withdrawn from the UK market so could increase the use of diquat and could subsequently increase its resistance risk.
There are currently 27 weed species world wide that have been identified as resistant to bipyridilium herbicides, including 20 dicotyledonous species (Heap, 1997), however resistance is fairly limited and many alternative products are available making this group a fairly low risk category.
Potential UK resistance risk: Low (*provided glyphosate remains available*)

5) Synthetic auxins (eg. 2,4-D, MCPA)

The growth regulator herbicides are easily translocated within the plant and cause excessive cell division leading to plant death. Only small quantities are required as a foliar application and they are transported rapidly deep into the roots. There is a very small amount of residual activity via the roots. However, one slight disadvantage is that they only kill the roots attached to living shoots at a certain growth stage, therefore due to the variable growth stages of weed populations not all plants may be as effectively controlled by these herbicides (Zimdahl, 1999), and multiple applications may be required. MCPA and 2,4-D are very similar in performance and used for generally the same target weed species. MCPA is more persistent in soil (2 to 3 months) and is used more widely in the UK, compared to 2,4-D that persists in the soil for 1 month only and is generally used more widely in Europe. Due to their lack of soil persistence they have a low mammalian toxicity and environmental risk. Mecoprop is another commonly used product in this herbicide group and was introduced to Europe primarily to control common chickweed and cleavers, however resistant chickweed populations have now been reported to this herbicide (Putwain & Mortimer, 1989).

The introduction of the synthetic auxins in both the UK and America back in the 1940's was a major revolution of weed control, as they had the ability to kill a wide range of both perennial and annual weed species without effecting the cereal or grass crop (Zimdahl, 1999). They were cheap to buy and easy to apply at low water volumes, making them extremely convenient for growers. Since their arrival the synthetic auxins have had widespread use for broad-leaved control across the world. Despite this heavy long-term usage relatively few resistant weed populations have evolved (Heap, 1997). Currently 25 species in total have resistant biotypes recorded worldwide (Heap, 2007). Of these, synthetic-auxin-resistant common poppy (*Papaver rhoeas* L.) in Spain, wild mustard (*Sinapis arvensis* L.) in Canada, mayweed (*Matricari perforata* Merat) in France and UK and common chickweed (*Stellaria media*) in 9 countries and the UK. On public rights-of-way in

Canada, where repeated use of 2,4-D has occurred, wild carrot (*Daucus carota* L.) has become resistant.
Potential UK resistance risk: Low

6) Dinitroanilines (eg. Trifluralin, pendimethalin)

This group of herbicides are cell division inhibitors and are used to control predominately grass and some broad-leaved weeds in a range of arable and horticultural crops. They are very distinctive due to their bright yellow colour and are all liquid compounds with low water solubility. They are generally used as pre-emergence herbicides, as their activity is required before seed germination of the target weed, and have been described as root growth inhibitors (Zimdahl, 1999). Some of the dinitroanilines are very volatile and therefore require soil incorporation post-application to ensure they are in the rooting zone of the weed for effective uptake. They are generally poorly translocated in the plant and do not leach from the soil, therefore soil persistence problems can occur.

Dinitroaniline herbicides have been used for over 30 years and although they are often used extensively and can have long soil persistence, very few cases of resistance to this group of herbicides have been identified. Heap (1997) reported five monocotyledonous and one dicotyledonous weed species that were resistant to dinitroaniline herbicides, all in America or Canada.
Potential UK resistance risk: Low

7) Gylcines

Glyphosate is a non-selective (amino acid biosynthesis inhibitor), foliar herbicide, with almost no soil activity due to rapid absorption therefore only used post-emergence. It is well translocated within a plant and initially inhibits EPSP synthase, but has the secondary function of affecting the synthesis of proteins, respiration and photosynthesis (Zimdahl, 1999). It is most effective on small plants and symptoms are visible after 7 to 10 days, making it slower acting than paraquat (1 to 2 days). Glyphosate has very low mammalian toxicity.

Resistance to glyphosate had only been recorded in one grass weed species, annual or rigid ryegrass (*Lolium rigidum*) in Australia in 1996, despite the widespread use of this herbicide for weed control on arable land and amenity areas worldwide. It was therefore considered as a low risk herbicide from a resistance point of view (Heap, 1997), which may be due to its mode of action, lack of residual activity in plants, and chemical structure. However, ten year later, by 2007, the number of weed species recorded as resistant to glyphosate was 13 (Heap, 2007), of which 8 species are broad-leaved weeds, listed in Table 3.

Table 3. The broad-leaved weed species with reported glyphosate resistance worldwide (Heap, 2007).

Species	Common name	Country	Year 1st found
Amaranthus palmeri	Palmer Amaranth	USA	2005
Amaranthus rudis	Common Waterhemp	USA	2005
Ambrosia artemisiifolia	Common Ragweed	USA	2004
Ambrosia trifida	Giant Ragweed	USA	2004
Conyza bonariensis	Hairy Fleabane	South Africa Spain	2003
		Brazil	2004
		Colombia	2005
		USA	2006
			2007
Conyza canadensis	Canadian fleabane	USA (17 states)	2000-2007
		Brazil	2005
		China	2006
		Czech Republic	2007
Euphorbia heterophylla	Wild poinsettia	Brazil	2006
Plantago lanceolata	Buckthorn Plantain	South Africa	2003

It has been considered that the introduction of glyphosate tolerant crops, in the early 1990s, predominately in the USA, was one factor that has led to the rise in the number of glyphosate resistant weeds. This is particularly apparent with Canadian fleabane (*Conyza canadensis*), as the increased number of reported cases of glyphosate resistance in this weed species is related to the increase in use of Roundup ready soybean (Figure 3). In the States of Indiana and Ohio glyphosate-resistant biotypes of Canadian fleabane have been reported in 29 and 20 counties respectively (Loux *et al*., 2006). In the Northern Central region of America, Roundup Ready soybean includes 81% of the varieties sown and approximately 60% of these crops are in a non-tillage situation with the sole use of glyphosate as herbicide control (USDA NASS, 2003). Management practices, which have increased the resistance pressure and contributed to the inadequate control of Canadian fleabane, include a lack of crop rotation, little or no-tillage systems, and the over-reliance on one herbicide (Loux *et al*., 2006). The role of cultural control in reducing or delaying selection pressure has long been known, irrespective of herbicide mode of action (Putwain & Mortimer, 1989; Reed *et al*., 1989).

Glyphosate is used extremely widely in the UK for amenity weed control, due to its high levels of control, low environmental risk, and cost effectiveness. Currently no cases of resistant weeds have been reported in the amenity sector.

Potential UK resistance risk: Medium? (*could change after paraquat withdrawal*)

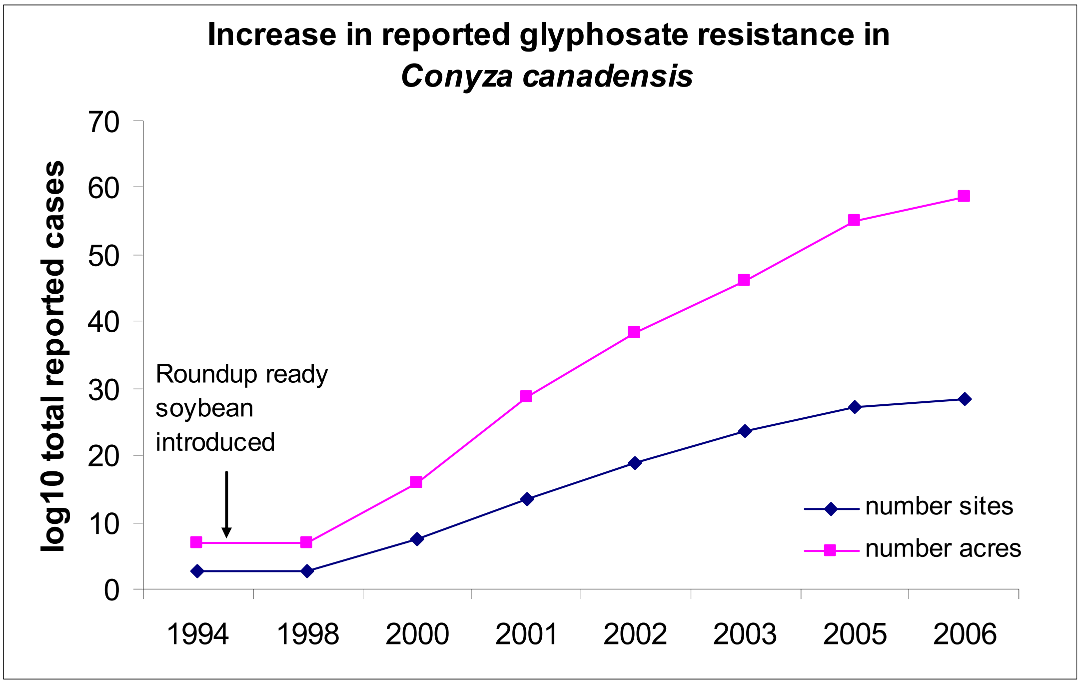

Figure 3. The increase in the reported cases of glyphosate-resistant *Conyza Canadensis* related to the increase in acres sown with Roundup Ready Soybean in the USA (*data from ISHRW and USDA statistics website for 2005-06*).

8) Triazines

Triazine-resistant weeds in Europe, although featuring prominently in the worldwide herbicide-resistance database, are not considered to be a major problem in Europe now. In 1978, triazine-resistance accounted for 67% of the recorded herbicide resistance. By 1997, 61 weed species had evolved resistance to triazine herbicides, accounting for only 16% of all recorded resistant-biotypes (Heap, 1997). Due to the vast amount of literature available on triazine-resistance, and their withdrawal from the market from January 2008, they will not be covered in this particular review.
Potential UK resistance risk: Formerly high, now uncertain

Triazinones have a similar mode of action to triazines, and are still available in the UK (eg. Metribuzin). Metamitron-resistant *Chenopodium album* (fat hen) has been detected in Belgium in sugar beet (Mechant *et al*., 2005). Recently, one suspected case has been reported in the UK (Pers comm., 2008). In Belgium it is uncertain how many resistant populations were selected by metamitron, as compared to the triazines, such as atrazine, used in maize. Seeds may have been transferred in slurry. Resistant populations in Belgium show cross-resistance between triazines (eg. Atrazine) and triazinones (eg. Metamitron). Consequently, triazines/triazinone resistance remains a threat in the UK, at least in sugar beet.

9) Other herbicides

There are a number of other herbicides from a range of groups that are commonly used for grassweed control, but do have activity on certain broad-leaved weeds. These would include ai's such as propyzamide, flufenacet, picolinofen, metazachlor and carfentrazone. As this review is focusing on broad-leaved weeds no further detail on these particular ai's will be given, however they need to be considered when assessing risk as part of a rotation as they may have a valuable role to play at potentially reducing the risk posed by other herbicides.

1.5 Cultural factors affecting resistance

There are a number of cultural factors that could influence the risk of herbicide resistance developing or increasing where already present. The rotational use of cultivations, cropping, sowing dates and chemistry is not a new concept for sustainable weed management strategies (Putwain & Mortimer, 1989), but often not practised according to the best advice. Weather conditions may also influence the sowing date and cultivation choice within a given season, so control of these factors is not always flexible and must be guided by the farmers' knowledge of their individual fields and local weed problems.

1.5.1 Cropping

The use of rotational cropping will provide an opportunity to potentially use a different type of cultivation, alternative sowing date (such as a brassica crop or a spring sown crop) and the use of alternative chemistry within crop. With a continuous crop the weed control may become unsustainable, as the same weeds will germinate and the risk of resistance developing will be higher. This is particularly a problem with grass weeds in the UK in areas where winter cereals are the most productive crop and in these situations crop rotations are generally adopted, but these are often very simple (eg. Wheat, wheat, oilseed rape). However, in the USA where Roundup Ready crops have been introduced and are sown on the same fields continuously cases of increased resistance have been reported (eg. Canadian fleabane), as discussed in the previous section.

1.5.2 Sowing date

The use of rotational cropping would also provide opportunities to alter the sowing date of crops, which in turn would affect the weed emergence patterns. This could be particularly favourably where predominately winter sown crops are grown resulting in a weed burden of autumn germinating species including chickweed and poppy, which are a resistance threat. Spring cropping would alter many of the weed species present, give crops a competitive advantage, and might allow the use of different herbicide chemistry, overall reducing the resistance risk. The autumn germinating weed species would then remain in the seed bank for longer, again reducing the resistance pressure.

1.5.3 Cultivations

The choice of cultivations will have a major affect on the weed seed bank dynamics. Ploughing inverts the soil to a depth of 20cm to 25cm resulting in surface shed seed from the current harvest year being buried below a depth that seed will germinate and older seed returning to the soil surface. This has many benefits for reducing the risk of herbicide resistance building up as the seed bank is constantly being diluted. However ploughing is a more expensive and time-consuming cultivation method and practically is often used on a rotational basis. Minimum tillage is often a more favoured option for cultivations as it is much cheaper and quicker than ploughing. Any seed shed that harvest year remains near the soil surface and is likely to germinate again the following season. This can result in a rapid build-up of certain weed species with a few seasons, putting more pressure on herbicide control and obviously increasing the resistance risk. The use of a stale seedbed technique, either after ploughing, but more commonly after minimum tillage can have a big advantage in terms of reducing the weed burden within the crop and subsequently can reduce the herbicide requirement and resistance pressure. This is particularly favoured where grassweeds, such as black-grass are present with a high resistance risk, as they tend to germinate rapidly once stimulated by cultivations. This method may not be as successful for many broad-leaved weeds that can have a more protracted germination period, but could be considered, particularly ahead of a spring crop in a situation where the risk is high. The depth of cultivation will also affect the weed species that germinate as each species has different requirements. Generally the smaller seeded weeds germinate from shallower depths, when the temperature and moisture requirements are suitable.

1.6 Basic genetics of Herbicide Resistance

There are many different modes of herbicide resistance and inheritence of these resitant traits varies. Resistance is most often conferred by a single nuclear gene mutation as in the case of ALS inhibiting herbicides. In contrast, photosystem II inhibitors (herbicides like atrizines and triazines) work at the chloroplast level and this has allowed a herbicide resistance gene to develop in the chloroplast genome. Whereas nuclear genes are inherited in a Mendelian fashion, chloroplast genes are inherited through maternal transmission only, although effects may be moderated by nuclear genes (Hurst, 1994). The factors involved in transmission of herbicide resistance are therefore likely to be different for Photosystem II herbicides (C1 group) and these herbicide cases were removed from the analysis when appropriate.

1.7 Mechanisms of resistance

There are two main mechanisms of resistance, enhanced metabolism and target site resistance. Enhanced metabolism (EM) resistance is the detoxification of the herbicide by the plant, leading to poor control, but usually partial resistance. EM resistance is the most common resistance mechanism for grass weeds in the UK. Target site resistance (TSR) is the blocking of the target site of herbicide action within the plant resulting in the plant surviving a dose of herbicide, which is usually complete resistance. In the UK two types of TSR have been identified, one affecting ACCase inhibitors (grass weeds) and another affects ALS inhibitors (broad-leaved and grass weeds). There are also likely to be other, as yet uncharacterised, mechanisms present.

In herbicide resistant broad-leaved weeds the majority of cases are TSR, with a few exceptions (eg. ALS metabolism (Hall *et al*., 1997)). This contrasts greatly with grass-weeds, such as black-grass and Italian rye-grass where EM resistance is possibly more important than TSR. This is a critical difference to be noted. It may just be that EM resistance in broad-leaved weeds has simply not been investigated in detail, but more likely due to the fact that grass-weeds are the same family as cereals and EM is the main detoxification method in cereals for selectivity.

2. Statistical exploration of biological factors affecting resistance

The statistical work, which follows in this section, explores both the contribution of herbicide and certain biological factors to the risk of developing herbicide resistance in broad-leaved weeds. Two possible types of herbicide effects are identified, depending on the location of the herbicide action in the cell.

In addition the effect of certain biological factors, including plant density, number of generations per season, seed production, type of fertilisation, weed longevity and seedbank numbers, polyploidy, and the interaction of lifecycle and cultivations are explored. Some of the biological factors which appear to have significant contribution to herbicide risk development are then looked at more closely in a subset of weeds, most of which are from the same family (Amaranthacae) but show different resistance risk, with a further four species, fat hen, poppy, chickweed and cleavers which are important to UK field crops.

There is a great deal of variation in the number and types of occurrences of herbicide resistance in weeds, so analyses to explore the biological factors that may increase the probability of a weed developing resistance to a particular herbicide were undertaken in this section of this review.

2.1 General overview of ISRW database from the weeds perspective

Analysis method

The most comprehensive list of reported herbicide resistance cases in broad-leaved weeds occurs in the International Survey of Herbicide Resistant Weeds database (ISHRW) (Heap, 2007) including 75 grasses and 129 broad-leaved weeds. A 'case' refers to a reported resistance incidence on this database. These grow in a variety of crops and locations across the world. Only data for broad-leaved weeds were used in the analysis for this review, which was broken down into two parts. Firstly the general risks from different types of herbicides was analysed for all the broad-leaved weeds. Secondly the biological factors, which may increase risk of herbicide resistance occurring, were examined in terms of this global dataset, before the subsets were examined more closely. Selections of these data are presented below.

2.2 Herbicides

Modes of action

For broad-leaved weeds alone the number of different species within the total number of reported herbicide-resistant cases are shown below (Figure 4) grouped according to herbicide mode of action. This highlights that for many of the modes of action (eg. ALS-inhibitors), although there are nearly 200 resistant cases reported, only approximately 50 different species are involved.

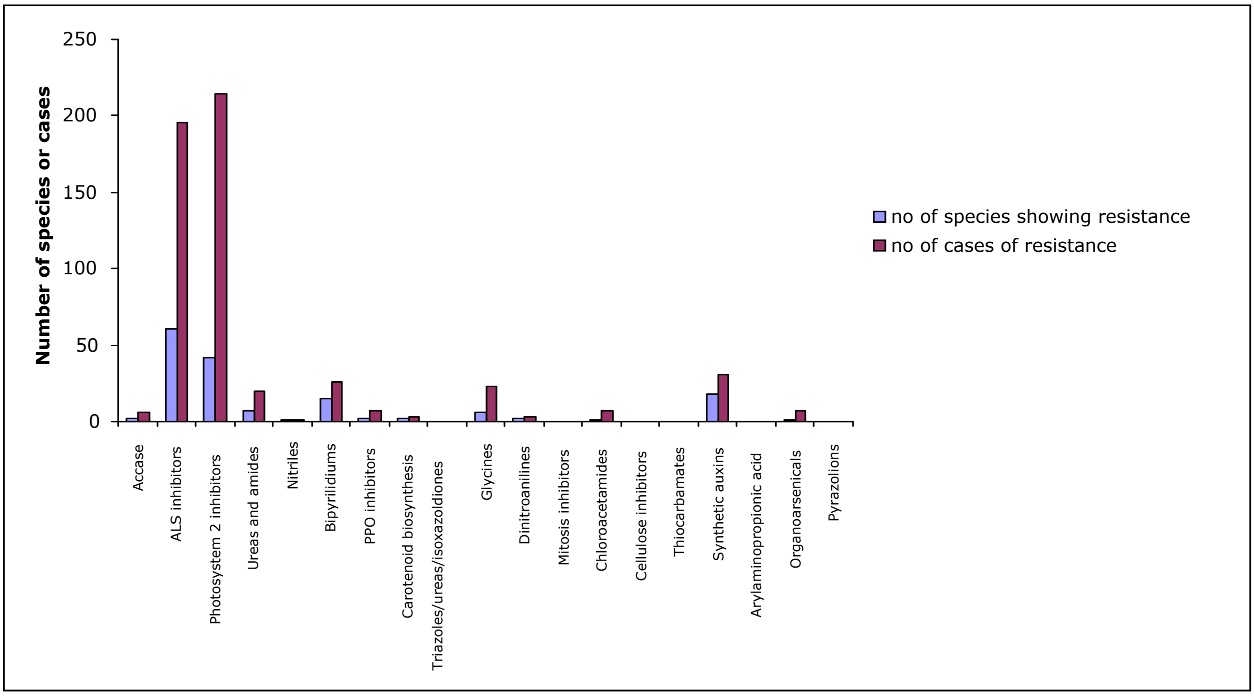

Figure 4. The number of herbicide-resistant broad-leaved weed species and total number of reported cases (*this could include multiple numbers of one species in different geographical locations*) of resistance for each different herbicide mode of action.

The total number of cases of resistance correlates moderately well with the number of modes of action (r = 0.713) (Figure 5). Each dot here represents a different weed species from ISRW. Some of the species have developed resistance to a wide range of herbicides, for example *Ambrosia artemesifolia* has developed 15 total cases of resistance against 5 different types of herbicide, while other species, such as fat hen have had more reported herbicide resistance cases, but against fewer herbicides. Both of these weeds are found in the same types of crop, for example sweetcorn in the United states, so may be expected to have been exposed to similar herbicide treatment regimes. The resulting differences are considered further in the case studies section. However, the increase of number of modes of action as the number of herbicide resistant cases for one particular weed increases could also be due to reporting issues. As the number of cases of resistance for a weed are reported globally it may lead to more people investigating that weed and subsequently finding more modes of action it is resistant to. This is just speculation, but needs to be considered when interpreting these data.

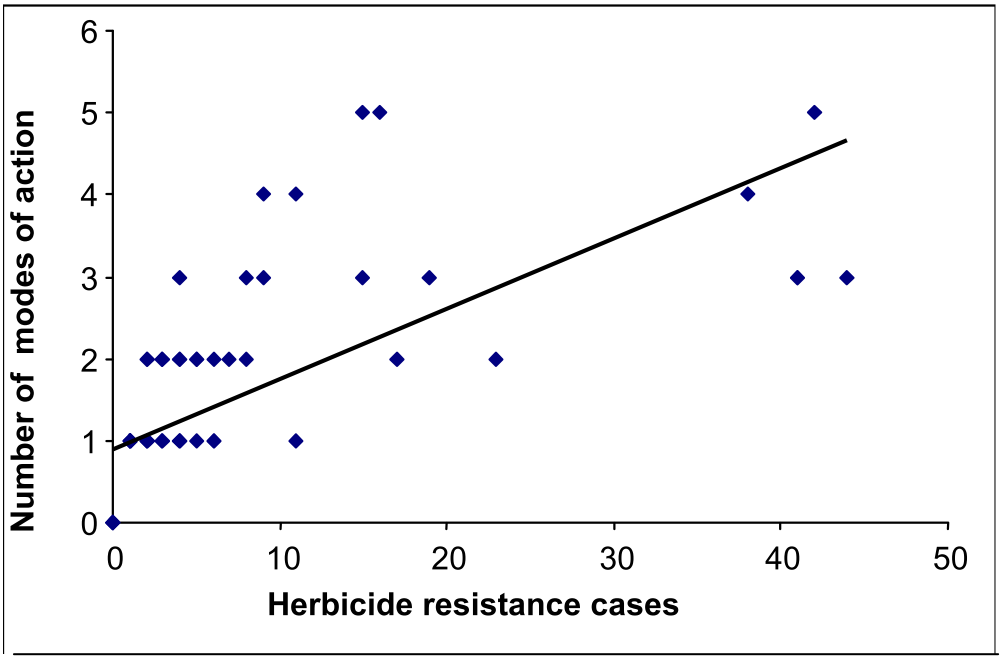

Figure 5. The correlation between total cases of resistance and the number of modes of action (each dot on the graph is a different weed species).

Genetic effects on herbicide resistance

The different ways that resistance to herbicides can develop have been considered in section 1 and appendix 2 of this review. It has been highlighted that the factors involved in a weed developing resistance to the photosystem II herbicides (group C1) may be different to those where nuclear inheritance is likely. Therefore the C1 group has been treated separately in these analyses.

Numbers of resistance cases

Weeds were ranked by total number of herbicide cases reported. The top broad-leaved species are shown in Table 4. Common poppy and chickweed have been included for comparison. Common poppy, with 7 herbicide cases is joint 17th ranked on the list, and then 10th when C1-resistance cases are removed. Common chickweed did show resistance to C1 herbicides but is still low on the list. A complete list of all the weeds is presented in Table 1 Appendix 1.

Table 4. The top broad-leaved weed herbicide resistance cases reported (*figures in parenthesis show the ranking*)

			Herbicide type	
Species	Common name	Total cases	C1	All other herbicides
Amaranthus retroflexus	Redroot Pigweed	44(1)	27(2)	17(4)
Conyza canadensis	Horseweed	42(2)	11(7)	31(1)
Kochia scoparia	Kochia	41(3)	14(4)	27(2)
Chenopodium album	Lambsquarters, Fat hen	41(3)	37(1)	4(22)
Amaranthus rudis	Common Waterhemp	38(5)	12(6)	26(3)
Amaranthus hybridus	Smooth Pigweed	23(6)	18(3)	5(17)
Amaranthus powellii	Powell Amaranth	19(7)	11(7)	8(8)
Xanthium strumarium	Common cocklebur	17(8)	0(43)	17(4)
Ambrosia artemisiifolia	Common Ragweed	15(10)	3(14)	12(7)
Senecio vulgaris	Common Groundsel	15(10)	13(5)	2(29)
Amaranthus palmeri	Palmer Amaranth	11(12)	4(10)	7(10)
Solanum nigrum	Black Nightshade	11(12)	11(7)	0(89)
Papaver rhoeas	Corn Poppy	7(17)	0(43)	7(10)
Stellaria media	Common Chickweed	4(29)	3(14)	1(45)

Even when the photosystem II inhibitor resistance cases are removed 75% of the first 15 resistant weeds still rank in the top 14 positions. Of most importance is the change in position of Fathen (*Chenopodium album*), which without the C1 resistance cases only shows four other reported cases. This suggests that in comparison with the other high ranking weeds Fat hen resistance cases are dominated by triazines. An important British arable broad-leaved weed, Cleavers (*Galium aparine*) does not rank in the list at all because no cases of resistance in this weed have been reported to the ISRW. Results were presented by Lutman & Lovegrove (1985) who studied 10 populations of cleavers that had been heavily exposed to the herbicide mecoprop. Some minor variations in control levels were reported, but no herbicide resistance.

2.3 Biological factors

Background

Random mutation in some plant genes can lead to changes in biochemistry, allowing plants with certain mutations to survive application of particular herbicides at rates that kill plants lacking those mutations. Mutations may confer changes to enzyme target sites reducing or preventing herbicide binding, they may increase metabolism and/or elimination of herbicides in target plants, or they may cause other physiological changes (eg reduced herbicide translocation, reduced uptake), allowing those individuals with resistant allele(s) to survive herbicide application, while most of the population is controlled. Thus with continued herbicide application, selection pressure ensures that resistant alleles are more likely to be successful and spread through the population. An instance of resistance is more likely to be reported when large numbers of resistant individuals are visible in the field. Low numbers of survivors are unlikely to be spotted in an arable field and their presence could be attributed to miss spraying. Several biological factors contribute to the successful transmission and retention of resistant traits in the weed population (for example large numbers of offspring, out-crossing, high competitiveness with crop).

The following factors are considered in this section of the review as key factors that may have an influence on resistance occurring in any weed species.

(i) Seed number per plant
Large numbers of offspring increase the chances of mutant alleles surviving and spreading through a population.

(ii) Plant density
A high plant density will increase the chance of a mutation conferring resistance being present in the population. However individual plants at high densities may have reduced seed numbers compared to lower density situations (Van Aker *et al*., 1997), and this may in turn reduce the rate of spread of mutant alleles within the population.

(iii) Number of generations per season
A greater number of generations per season will enhance the potential increase and spread of a resistant population. However, in the UK most arable broad-leaved weeds have only one generation per season.

(iv) Type of fertilisation
The spread of a resistant trait may be faster in out-crossing mating systems when resistance is conferred by single dominant nuclear gene. Chloroplast inherited traits may not be so affected unless hybrid vigour makes seed return per generation higher with out-crossing. Some species are self-fertile while others are self-sterile. However, even when plants are self-fertile the rate of development of male and female organs may differ, so plants may be more likely to outbreed.

(v) Seed longevity and seedbank size
The size of the weed seedbank is controlled by the number of seeds shed per plant and the plant density (considered above), their incorporation into the soil, seed longevity and mortality from causes such as predation, or loss to soil depth. In arable fields cultivations have a large influence on seed longevity whereas in amenity situations, seeds are usually shed to the surface where fungal infection, predation, and natural burial are more important.
The weed seedbank will also affect the proportion of plants that show herbicide resistance at any time. Initially a large seedbank of non-resistant seeds at germination depth may out-compete the resistant seed, reducing the chance of plants reaching maturity. This will slow the development of the resistant trait in the population (Cavan *et al*., 2004). Conversely a large resistant seedbank of long-lived seeds can constantly refresh a non-resistant population making resistance problems persistent in spite of changes in management methods.

(vi) Polyploidy

Simple species have a basic chromosome number per plant. During evolution the number of chromosomes has sometimes increased so that copies of individual chromosomes have been retained. More chromosomes mean that there are more genes, and since the risk of mutation depends on the number of genes the chances of a mutation occurring in a larger genome is increased. But the effects of polyploidy are complex. If a gene, conferring some sort of herbicide resistance characteristic is dominant, that is, its effects are not masked by other active genes on a replica chromosome, then the chance of a mutation occurring that is immediately expressed in the population will increase. In other cases a recessive gene mutation may be masked for many generations.

(vii) Interaction of lifecycle and cultivations
The weed species must be able to complete its life cycle within the crop and cropping season for seed return to occur. For this reason weed species in a field are often dependent on the type of crop, in a spring crop orache or fat hen will be dominant, as they germinate at the same time as the crop and are not smothered by it as it grows. They are seldom found as infestations in a winter rotation. In the amenity situation the ground disturbance becomes important, and species may grow preferentially on disturbed or open soil and are not able to compete with established turf. Plants must complete their life cycle before disturbance occurs.

(Viii) Seed dispersal
Wind dispersed seeds can travel further and this may account for the rapid geographical spread of invasive species like Canadian fleabane.

Analysis methodology of biological factors
Large amounts of biological data were collected for each of the species in the ISRHW database. A variety of data sources including the Weed Manager database, refereed papers, and the Ecological Database of the British Isles (**http://www.york.ac.uk/res/ecoflora/cfm/ecofl/index.cfm**) provided information on seed numbers, fertilization and flowering periods. Data were available for about 60% of the broad–leaved weed species.

(i) Seed production
Data for maximum, minimum or a mean number of seeds per plant for each species (total of 56 species) was transformed by log10, so that data could fit on a reasonable scale. Where only maximum and minimum data were available the average of the log was used. These data are plotted in Figure 6 against the number of reported herbicide resistant cases. Each spot on the graph represents a single species, so each species is represented twice, either with photosystem II or all other herbicides. The arrows point to fat hen, which has the highest number of herbicide resistance cases reported for Photosystem II herbicides.

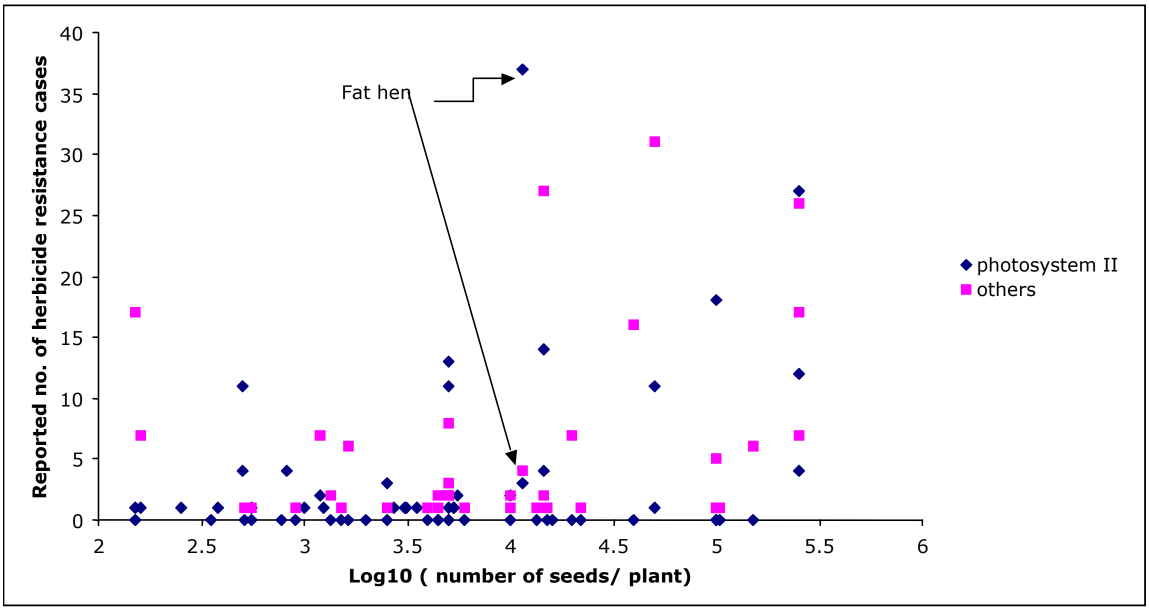

Figure 6. Reported herbicide resistance cases for photosystem II herbicides and all other herbicides v log10 number of seeds/plant. Each spot on the graph represents a single species from a total of 56 species.

These data suggest that plants that produce larger numbers of seeds per plant are more at risk of developing herbicide resistance.

(ii) Type of fertilisation
Available data on pollination of species were variable. Information was available about the proportion of self-fertilised seeds, the rate of maturation of flowers and if plants were monoecious (with only one sex per plant) or dioecious (both sexes on each plant). This led to the use of the following categories: fully out-crossing (out), fully self-crossing (self), mostly out-crossing (mostly out), or mostly self-crossing (mostly self) and results are presented in Figure 7. The majority of the resistance cases occurred in out-crossing weeds. However where species were fully self-fertilised there were 8% more photosystem II herbicide resistance cases.

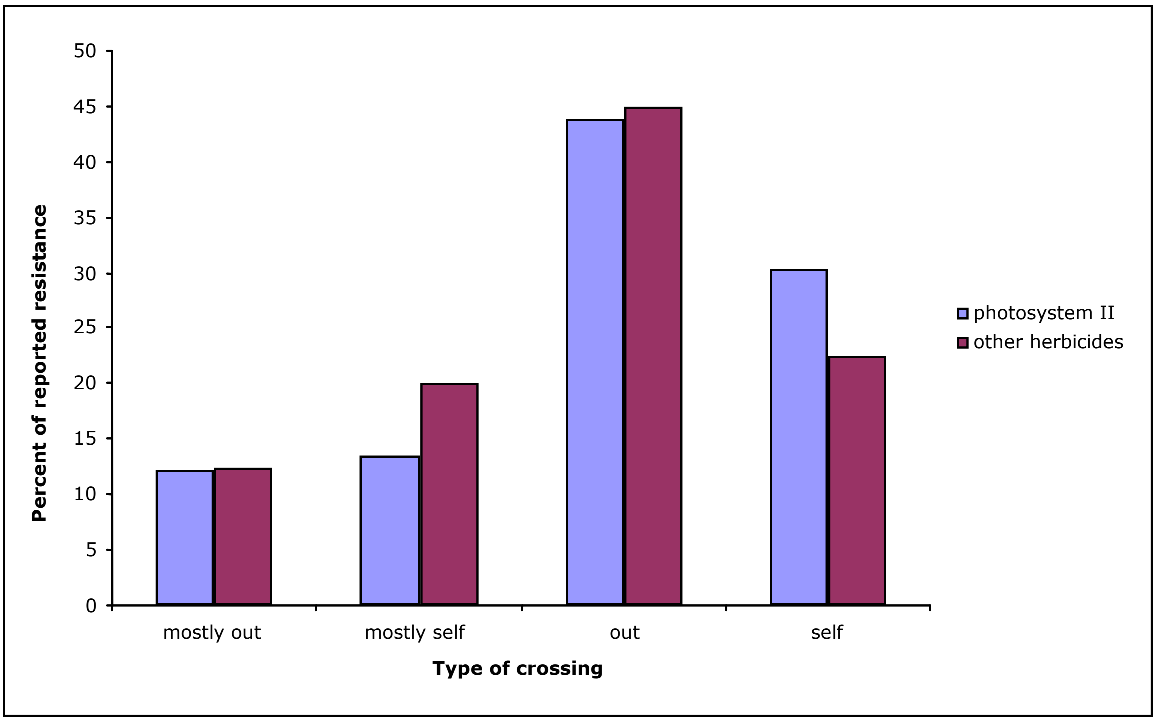

Figure 7. The number of herbicide resistant cases of broad-leaved weeds that were either out-crossing alone, self-crossing alone or mostly out-crossing or mostly self-crossing.

This suggests that with herbicides whose resistance is conferred by nuclear genes (the majority of current herbicide use) out-crossing species may develop resistance faster. If herbicide resistance is conferred by cytoplasmic genes, as in the case of photosystem II herbicide resistance (triazines), purely self-crossing species may have an important role to play. However, this could simply be due to the fact that most weeds are out-crossers, making this factor difficult to accurately interpret.

iii) Number of flowering months

There was ample available data for the period for which species flowered. Because this may include the north or south hemisphere the data were recalculated as number of available flowering months. These were plotted against the number of reported herbicide resistance cases. In this graph each spot in a series represents one species. The analysis shows that there was no relationship between these two factors (Figure 8). Plants such as Common chickweed, which flower every month of the year, have reportedly few herbicide cases, while *Amaranthus retroflexus,* with over 40 reported cases of resistance in America, flowers for no more than 5 months a year.

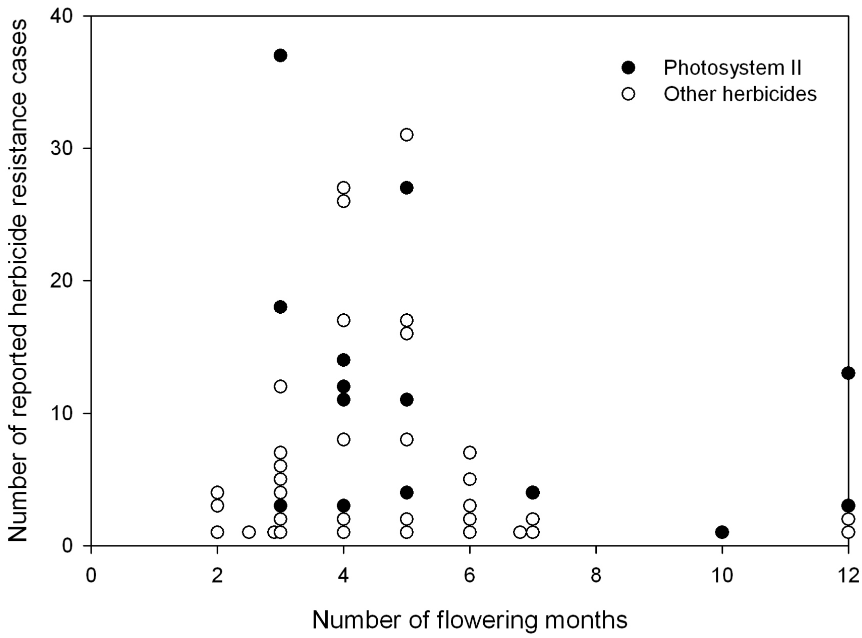

Figure 8. The number of flowering months plotted against the total number of resistance cases.

(iv) Plant density
It was difficult to find data on typical weed numbers in the field and indeed this varies with husbandry so that this route was not pursued with the dataset.

(v) Polyploidy
Chromosome numbers were plotted against the number of reported herbicide resistance cases where data was easily available. If more than one chromosome number was reported the numbers were averaged. There was no significant correlation.

(vi) Seed longevity and seedbank size
Longevity and mortality of many worldwide plant seeds were reviewed by Thompson *et al.*, (1997). They showed a wide range of methods used to experiment on weed longevity, a major problem being the length of the study. In many cases the experiments were terminated before all the seeds had died. Many different methods have been used, often including burying seeds in packets which are not representative for true conditions. Within their database, it is possible to see that even when the same methods were used with one species but different authors, there was a wide range of longevity and relationships between different species was not always of the same order, therefore very unreliable. Different cultivations result in different seed longevities, for example where the soil was mixed thoroughly several times a year, poppy seeds suffered mortality of 93% over 6 years compared to 79% in undisturbed soil (Roberts and Feast 1993) while Salisbury (1961) has reported lifetimes in excess of 40 years. In general broad-leaved weed seeds have greater longevity than monocotyledons; for example sterile brome seeds are unlikely to last for more than a year, although black-grass seeds may be viable for up to five years. The seed survival rates for chickweed and poppy

are both very different, however they have both developed resistance. Because of all this variability it was not considered feasible to include seed longevity in the statistical analysis of this project.

(vii) Number of generations per year
Seed return per generation was multiplied by the number of generations per year to estimate the annual seed return, which would predict the rate of herbicide resistance development. Data for individual weed species is patchy, although common chickweed is known to have up to 6 generations per year and some autumn germinating *Chenopdium polyspermum* has been observed to set seed within 8 weeks of sowing (*pers ob*) thus giving rise to at least two generations within one year. However, this is without a crop present and there is little evidence that this might occur within a cropping situation. In the UK and Europe there is more likely to be only one generation per season in an autumn or spring-sown crop.

2.4 Summary of the statistical exploration of biological factors

As a result of the statistical exercise detailed above, two factors were found to be of importance in increasing the risk of developing herbicide resistance. These were seed production and out-crossing. Other factors were not found to be of importance or could not be explored in further detail within the scope of this review, however some species seemed worthy of more detailed analysis. These include the amaranth family, where there was a wide range of herbicide resistance; fat hen, mentioned above because of the difference in reported cases of photosystem II and other herbicide resistance; poppy and chickweed which both show resistance in the UK and Canadian fleabane which has become an increasing weed of amenity sites and vegetable crops.

2.5 Case study

The objective of the case study was to tease out the specific biology and cultivation effects that might have caused the differences in herbicide resistance developing in a particular weed species. The key species of interest are listed in Table 5.

Table 5. Reported herbicide resistance cases (*triazine resistant cases separated out*) Worldwide.

Species	Common name	Total reported herbicide resistant cases	*Triazine resistance*	Other Herbicides (**not triazines**)	No. of modes of action
Amaranthus albus	Tumble Pigweed	1	*1*	0	1
A. arenicola	Sandhills Amaranth	0	*0*	0	0
A. blitoides	Prostrate Pigweed	6	*4*	2	2
A. cruentus	Smooth Pigweed (Cr)	1	*1*	0	1
A. hybridus	Smooth Pigweed	23	*18*	5	2
A. lividus	Livid Amaranth	4	*2*	2	3
A. palmeri	Palmer Amaranth	11	*4*	7	4
A. powellii	Powell Amaranth	19	*11*	8	3
A. quitensis	Pigweed (quitensis)	2	*0*	2	1
A. retroflexus	Redroot Pigweed	44	*27*	17	3
A. rudis	Common Waterhemp	38	*12*	26	4
A. tuberculatus	Tall Waterhemp	1	*0*	1	1
Chenopodium album	Fat hen	41	*37*	4	3
Conyza canadensis	Canadian fleabane	42	*11*	31	5
Papaver rhoeas	Common Poppy	7	*0*	7	2
Stellaria media	Common Chickweed	4	*3*	1	2

To reduce some of the inherent variation and because more data were available, the target weed group study was confined to the United States. Data on infestation levels; yield loss and cropping for this range of weeds are shown in Table 1, Appendix 2. Poppy and chickweed are not extensively weedy in the United States and so have no calculated infected area. Further detailed biological and ecological data are shown in Tables 2 and 3, Appendix 2. Due to many members of the Amaranth family developing herbicide resistance it was considered that this group would be studied in more detail.

2.5.1 Amaranths

Members of the amaranth family form a group of major weeds of spring crops in the United States and Canada, infesting both corn and soya bean. Data were available on cropping production, location and resistance for this weed group in some detail.

The amaranths are generally a very complex group of weeds and it is often difficult to tell species apart. Recently some of the species have been renamed, and regrouped. Although species may be separated in the ISRW database, the USDA database treats *A. rudis* and *A. tuberculatus* as the same species. Other botanists treat *A. cruentus* as the same species or a sub species of *A. hybridus. A. lividus* has been renamed/regrouped as *A. blitum.*

Geographic spread and herbicide resistance status

The geographic area and crops in which each resistant species has been found are summarised in Table 6. Most of the crops species for the target group are spring-sown crops, all the amaranths and fat hen are spring germinating, but Canadian fleabane mainly germinates in autumn, although a small proportion may germinate in spring (Wu *et al*., 2007). The resistant biotypes of spring germinating species are found in spring-sown crops in the USA, or in situations like orchards or vineyards in Europe. Canadian fleabane shows multiple herbicide resistance in soybean but many of the recently reported resistance cases are to glyphosate, so that perennial crops (cotton and blueberry) are also involved. The influence of roundup-ready crops has already been discussed in section 1.4 of this review.

Table 6. The types of crops infested by the Amaranth species

Species	Common name	States
Amaranthus albus	Tumble Pigweed	Found in winter and spring crops in Canada
A. arenicola	Sandhills Amaranth	
A. blitoides	Prostrate Pigweed	Found in winter and spring crops in Canada
A. cruentus	Smooth Pigweed (cr)	
A. hybridus	Smooth Pigweed	In corn and soy in USA
A. lividus	Livid Amaranth	In vegetables in usa
A. palmeri	Palmer Amaranth	Cotton,soy corn,cropland,alfafa in usa
A. powellii	Powell Amaranth	Vegetables, herbs and soy in USA
A. quitensis	Pigweed (quitensis)	NA
A. retroflexus	Redroot Pigweed	Found in winter and spring crops in canada
A. rudis	Common Waterhemp	Corn, soya, alfafa, sorghum in usa
A. tuberculatus	Tall Waterhemp	Soy in usa
Chenopodium album	Fat hen	Mainly corn, and in corn soy rotations
Conyza canadensis	Canadian fleabane	Soybean and cotton since 1994 in blueberry and amenity situations

The distributions of the individual Amaranth species are mapped in Appendix 4, Figure 1. Generally, the total number of reported resistance cases is in line with the proportion of the USA in which the weed is found. The plant which contradicts this is *A. albus*, (tumble pigweed) which is found everywhere in the USA but has only one reported herbicide resistance case. A general summary of the cropping area of the USA infested with resistant weed species is presented in Appendix 3.

A further pointer to the importance of husbandry in the development of herbicide resistant biotypes in this target weed group is the occurrence of Amaranth species in winter crops such as winter wheat, barley and oilseed rape in Canada (Costea *et al*., 2003). There is no report of herbicide resistance species in these crops in Canada.

Biological factors potentially influencing resistance

Herbicides are most often applied to weeds when they and the crop are small; to prevent competition as the crop develops. Therefore germination period of the weed at the same period as the crop could be an important contributor to development of resistance, see below.

This target group of weed species shows once again that seed number (Appendix 2, Table 2) is a predictor of the risk of developing herbicide resistance. However for this restricted dataset there seems no link between amount of out-crossing and development of either nuclear or cytoplasmic controlled resistance.

Final plant height may give an indication of the growth rate of the weed through the season. All Amaranth species grow fairly fast while *A. tuberculatus/rudis* grow more rapidly than the other amaranth species. The taller amaranths often have more reported herbicide resistance cases. However *A. cruentus,* which is a fairy tall weed, has fewer reported cases. This may be because of the greater influence of seed return.

The germination periods of the case study plants in relation to their host crop is given in Appendix 2, Table 3. As noted above most of the herbicide resistant species are found in spring crops.

2.5.2 General conclusions from the case study

The data available relating to reported cases of herbicide resistant Amaranth species highlights the importance of crop husbandry to the weed developing herbicide resistance. For example the number of cases is generally linked to the total area of the USA in which the plant is found. This would be as expected. However the rule is tested by *A. albus,* which occurs in crops all over the USA but with no cases of herbicide resistance reported in that country. In general the Amaranth species have developed resistance biotypes in crops germinating at the same time as the weed species. There was no evidence in this limited group of weeds that out-crossing was correlated to resistance development. In general the rule, that the greater seed number predicts the risk of herbicide resistance developing, holds good with this weed species. The rule is again tested by *A. albus*, which has a moderate seed number and this is difficult to explain. In this weed group plant height also appears to have an effect on resistance risk. Taller species had a greater chance of developing herbicide resistance. *A. albus* are among the lower growing species and may perhaps be protected from the herbicide application by their growth habit, or the rate of intake of nutrients. Another factor not considered so far may be the ecology of *A. albus*. This plant grows preferentially in arid and semi arid areas, and this may also affect nutrient and herbicide uptake.

3. Predicting the likely next species

It is fairly difficult to predict the next likely resistance risk to the UK, but by investing some of the key biological factors that are common in resistant weeds worldwide and understanding the risks some conclusions can be drawn.

3.1 Biological factors increasing the resistance risk

Botanical family

This factor is a poor predictor of resistance risk as there is no obvious link between resistance and weed family groupings.
Resistance risk: **Low**

Seed production

It is clear from the basic analysis using data from the ISHRW that seed production is an important factor in the worst herbicide resistance cases reported. Many of the herbicide-resistant weeds reported produce a high number of seeds per plant. As the number of seeds produced by a weed plant increases, so does the chances of a resistant mutation spreading within a population. Resistant weeds may also show fitness penalties compared to non-resistant types, and competition may decrease seed return of the resistant types.
Resistance risk factor: **High**

Seed persistence

Both seed dormancy and length of time that seeds remain viable may contribute to the persistence of a resistance event. Seeds that remain dormant for one or two seasons bearing herbicide resistance genes, will give rise to plants showing the resistance in later years, but it may be many years before a buried but viable seed is able to germinate. The data available are very unreliable to accurately use this factor to predict resistance risk, therefore making it a fairly poor predictor of herbicide resistance risk.
Resistance risk factor: **Low**

Pollination method

Another important factor appears to be method of pollination, although there is little evidence to prove which method of pollination leads to the most resistance risk. The majority of resistant weed species are cross-pollinators, however there are some species that are predominately self-pollinators, but do show some cross-pollination (eg. Common chickweed and Canadian fleabane).
Resistance risk factor: **Medium**

'Weediness'

The 'weediness' or vigour of an individual weed species is also an important factor in determining its resistance risk, as the vast majority of the resistant biotypes are very 'weedy' and competitive, including those discussed such as common chickweed, poppy, fat hen, Canadian fleabane and the *Amaranthus* spp.

Resistance risk factor: **High**

Two other factors are listed below that have not been included in the analysis due to lack of data, but are important when considering resistance risk.

Mobility

Potentially the more mobile a plant or seed the greater the chance of resistance spreading. For examples small lightweight, perhaps wind-dispersed seeds may have a higher risk than larger heavier seeds.
Resistance risk factor: **Medium**

Occurrence of resistance elsewhere/locally

If resistance is already present in neighbouring fields, farms or habitats then the risk of resistance occurring in that area is potentially greater.
Resistance risk factor: **High**

3.2 Chemical factors increasing the risk of resistance

It is well understood that rotation of herbicide chemistry can reduce the risk of resistance developing. The repeated use of single products on the same weed species has led to many resistant weeds, including the Triazines in orchards and vineyards and glyphosate on herbicide-tolerant crops. The biggest risks to broad-leaved weeds are the ALS-inhibiting herbicides as the rate of increase of reported resistance cases has increased dramatically since the start of the 1990's.

3.2.1 Repeated glyphosate use in amenity areas

In the UK Canadian fleabane is increasingly seen on railway lines and embankments and the most common herbicide treatment is a repeated application of glyphosate. There is a concern that this weed is therefore a high-risk species in terms of resistance development. However, that particular habitat is relatively undisturbed and newly shed seed is less likely to germinate readily without cultivation. Hence many seed are likely to senesce and it could be argued that due to its location this weed is at lower risk than those growing within a cultivated crop. It would be advisable for this species to be monitored in the UK and perhaps seed collected and tested where there is particular concern.

3.2 Prediction risk tool

From the information that has been discussed and analysed in this review on the biological and chemical risks for individual weed species it is possible to begin to create a list of important factors, to provide a guidance tool to aid the resistance risk/hazard (Table 7). For the purposes of this review this is just an outline of a proposed set of criteria and a full prediction matrix will be presented as a separate document.

Table 7. A list of important factors to be included in a prediction risk/hazard matrix of broad-leaved weed species developing herbicide resistance based on the biology of the weed and chemistry used for control (*predictions for the UK only*).

	Risk factors
Weed biology	Seed production
	'Weediness'
	Seed persistence/viability
	Previous cases
	Generation time
	Fertilisation method
	Cultural control options*
Chemistry	Mode of action
	Mode of use (repeated per season?)
	Any alternative modes of action?
	Intrinsic activity
	Residual activity

The resistance risk from the weed biology aspect can be modified by cultural factors* (as discussed in section 1.5 of this review). These include rotation of crop choice and cultivation method and manipulation of weed germination by altering the crop sowing date. The rotation of herbicide chemistry (especially including different modes of action) can also help to reduce the resistance risk. When multiple applications of the same chemistry are applied within one season, which may be the case with glyphosate applications in amenity areas, the resistance risk is increased. These factors should be considered within or along side any resistance risk matrix.

4. Discussion

This review aimed at determining the current status of herbicide-resistance in broad-leaved weeds worldwide. However, data are fairly limited and therefore it is important to consider that results only reflect the current status according to those data. The International Survey of Herbicide-Resistant Weeds, on the Weed Science website is an excellent source of global information and a very valuable resource that hopefully will be maintained. The limited number of key weed species where resistance has already developed were considered in relation to their population biology, 'weediness', and response to different herbicides. This analysis has provided an indication of some of the most important factors that can effect the risk of resistance developing or spreading rapidly once present. These include high seed production, seed persistence, plant vigour and competitiveness, and to some extent method of fertilisation, although this factor was not always consistent between species. Effects such as seed decline rate or seed persistence could explain why a very common weed such as *Galium aparine* (cleavers) has not developed resistance in the UK, despite relatively high levels of herbicide application (Lutman *et al*., 2002).

One major contributor to the development of resistance, particularly in the weed species commonly found in arable fields in the USA, such as the Amaranths and Canadian fleabane, was a lack of cultural control methods. Cultural control and rotational herbicide use should be the basis to any weed management strategy and for almost 20 years the same message has been emphasised by researchers aimed at reducing the selection pressure of herbicides to prevent or delay the onset of resistance (Reed *et al*., 1989; Kudsk *et a*l., 1995). In 1989 Putwain & Mortimer summarised the key tactics that should be adopted to delay the development of resistance in the short-term, which remain high priority today: - (1) A rotational use of herbicides with different modes of action should be used, (2) Use of mechanical cultivations used where possible to provide differential selection against resistant biotypes, (3) Where possible use herbicides that induced negative cross-resistance in situations where resistance to a particular herbicide is expected to evolve, (4) Act promptly and have resistance tests carried out in attempt to contain the problem. The longer-term strategies listed are also extremely relevant today and include (1) the retention of older herbicides to be used in rotations to control weeds resistant to new products (2) crop cultivars should not be used in the same rotation where they are resistant to herbicides with the same mode of action (ALS herbicides in particular). In general the use of crop rotations, herbicide rotations (different modes of action), mechanical cultivation, appropriate herbicide doses and timings are all still key factors for all herbicide resistance management strategies, and may delay or prevent resistance and retain the life of the ever-reducing number of herbicide products available.

When trying to identify the risk of an individual weed species' propensity to evolve resistance, related to their population biology, agroecology and 'weediness', the challenge is great, as many different factors are involved. However this review has emphasised a key aspect which is often overlooked, assessing the problem of herbicide resistance not only from the herbicide perspective but also taking into account the biology of the weed.

The second specific objective of this review involved identifying the risk imposed by different herbicides. The rotation of herbicide chemistry has been shown to reduce the risk of resistance developing in grass weeds (Clarke *et al*., 1997; Moss, 2004). The repeated use of single products on the same weed species has led to many resistant weeds, including the Triazines in orchards and vineyards in the UK and glyphosate on herbicide-tolerant crops in the USA. In the UK amenity weed control predominately uses repeated applications of glyphosate and therefore monitoring of control levels and particular weed species, especially Canadian fleabane on railway embankments, is essential to highlight any resistance issues at a very early stage. The biggest risks to broad-leaved weeds are the ALS-inhibiting herbicides as the rate of increase of reported resistance cases has increased dramatically since the start of the 1990's. Therefore careful planning of herbicide choice, timing of application to suit the weed growth stage, along with accurate doses, will help to get the best control from specific products.

Herbicide-resistance in broad-leaved weeds is an increasing problem globally, and within Europe and the UK, and the monitoring of high-risk weed species is now essential to help to manage the problem for the future.

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APPENDIX 1.

Table 1. The occurrence and distribution of ALS-Resistant broad-leaved weeds world-wide (updated in 2007 from Heap 1997).

Weed species	Common name	Herbicide/ group	First country and first year identified
Alisma plantago-aquatica	Common Waterplantain	Bensulfuron	Portugal (1995)
Amaranthus blitoides	Prostrate Pigweed	Sulfonylureas	Israel (1991)
Amaranthus hybridus	Smooth Pigweed	Imazaquin	USA (1994)
Amaranthus palmeri	Palmer amaranth	Imazethapyr	USA (1991)
Amaranthus quitensis	Pigweed (quitensis)	Imazethapyr	Argentina (1996)
Amaranthus retroflexus	Redroot Pigweed	Sulfonylureas	Israel (1991)
Amaranthus rudis	Common Waterhemp	Imazethapyr	USA (1993)
Amaranthus tuberculatus	Tall waterhemp	ALS inhibitors	USA (1998)
Ambrosia artemisiifolia	Common Ragweed	Imazethapyr	USA (1998)
Ambrosia trifida	Giant Ragweed	Imazethapyr	USA (1998)
Ammania auriculata	Redstem	Bensulfuron	USA (1997)
Ammania coccinea	Long-leaved loosestrife	Bensulfuron	USA (2000)
Anthemis cotula	Mayweed Chamomile	Chlorsulfuron	USA (1997)
Bacopa rotundifolia	Disc Water Hyssop	Bensulfuron	Malaysia (2000)
Bidens pilosa	Hairy Beggarticks	Imazaquin	Brazil (1993)
Bidens subalternans	Beggarticks- B. subalternans	ALS inhibitors	Brazil (1996)
Brassica tournefortii	Wild Turnip	Chlorsulfuron	Australia (1992)
Camelina microcarpa	Smallseed falseflax	Chlorsulfuron	USA (1999)
Chenopodium album	Lamsquarters/Fathen	Thifensulfuron	Canada (2001)
Chrysanthemum coronarium	Crown Daisy	ALS inhibitors	Israel (2000)
Conyza bonariensis	Hairy Fleabane	Sulfonylureas	Israel (1993)
Conyza canadensis	Horseweed	Sulfonylureas	Israel (1993)
Cuscuta campestris	Field Dodder	Sulfonylureas	Israel (1994)
Cyperus difformis	Smallflower Umbrella Sedge	Bensulfuron	USA (1993)
Damasonium minus	Starfruit	Bensulfuron	Australia (1994)
Descurainia sophia	Flixweed	Tribenuron	China (2005)
Diplotaxis tenuifolia	Perennial Wall Rocket	Chlorsulfuron	Australia (2004)
Echium plantagineum	Salvation Jane	Chlorsulfuron	Australia (1997)
Elatine triandra var.pedicellata	Mizohakobe	Bensulfuron	Japan (1998)
Euphorbia heterophylla	Wild Poinsettia	Imazethapyr	Brazil (1992)
Fallopia convolvulus	Black Bindweed	Chlorsulfuron	Australia (1993)
Galeopsis tetrahit	Common Hempnettle	ALS inhibitors	Canada (1995)
Galium spurium	False cleavers	ALS inhibitors	Canada (1996)
Helianthus annuus	Common Sunflower	Imazethapyr	USA (1996)
Iva xanthifolia	Marshelder	Imazamox	USA (2005)
Ixophorus unisetum	Pasto Honduras	Imazethapyr	Costa Rica (1988)
Kochia scorparia	Kochia	Chlorsulfuron	USA (1987)
Lactuca serriola	Prickly Lettuce	Chlorsulfuron	USA (1987)
Limnocharis flava	Yellow bur-head	Bensulfuron	Malaysia (1998)
Limnophila erecta	Marshweed	Bensulfuron	Malaysia (2002)
Limnophila sessiliflora	Asian Marshweed	Bensulfuron	Japan (1997)
Lindernia dubia	Low False Pimpernel	Bensulfuron	Japan (1996)
Lindernia dubia var. major	Low False Pimpernel (major)	Bensulfuron	Japan (1996)
Lindernia micrantha	Azetogarashi (Japanese)	Bensulfuron	Japan (1996)
Lindernia procumbens	Azena (Japanese)	Bensulfuron	Japan (1997)
Mesembryanthemum crystallinum	Ice Plant	Chlorsulfuron	Australia (2005)
Monochoria korsakoii		Sulfonylureas	Japan (1994)
Monochoria vaginalis	Arrowhead Monochoria	Bensulfuron	South Korea (1999)
Neslia paniculata	Ball Mustard	Metsulfuron	Canada (1998)
Papaver rhoeas	Corn Poppy	ALS inhibitors	Spain (1993)

Parthenium hysterophorus	Ragweed Parthenium	ALS inhibitors	Brazil (2004)
Pentzia suffruticosa	Calomba Daisy	Metsulfuron	Australia (2004)
Raphanus raphanistrum	Wild Radish	Chlorsulfuron	Australia (1997)
Raphanus sativus	Radish	ALS inhibitors	Brazil (2001)
Rapistrum rugosum	Turnipweed	Chlorsulfuron	Australia (1996)
Rotala indica var. uliginosa	Kikashigusa	Bensulfuron	Japan (1998)
Sagittaria guyanensis	Guyanese Arrowhead	Bensulfuron	Malaysia (2000)
Sagittaria montevidensis	California Arrowhead	Bensulfuron	USA (1993)
Sagittaria pygmaea	Dwarf Arrowhead	ALS inhibitors	South Korea (2004)
Salsola iberica	Russian Thistle	Chlorsulfuron	USA (1987)
Scirpus juncoides var. ohwianus	Inu-hotarui	Bensulfuron	Japan (1998)
Sida spinosa	Prickly Sida	Imazaquin	USA (1995)
Sinapsis arvensis	Wild mustard/Charlock	Chlorsulfuron	Canada (1992)
Sisymbrium orientale	Indian Hedge Mustard	Triasulfuron	Australia (1990)
Sisymbrium thellungii	African Turnip Weed	Chlorsulfuron	Australia (1996)
Solanum ptycanthum	Eastern Black Nightshade	Imazethapyr	USA (1999)
Sonchus asper	Spiny Sowthistle	Metsulfuron	Canada (1996)
Sonchus oleraceus	Sowthistle	Chlorsulfuron	Australia (1990)
Sorghum bicolor	Shattercane	ALS inhibitors	USA (1994)
Stellaria media	Common Chickweed	Chlorsulfuron	Denmark (1991)
Thlaspi arvense	Field Penny Cress	Trifensulfuron	Canada (2001)
Xanthium strumarium	Common Cocklebur	Imidazolinones	USA (1989)

APPENDIX 2

Table 1. Agricultural information, % cropping area infested and Yield losses from the target weed group in the USA

Species	Common name	% crop area with resistant weeds	Notes	Yield loss		
				Wheat	Sweetcorn	Soya
Amaranthus albus	Tumble Pigweed	N/A	Weed in all areas		34% loss @ 5 ppm hadss	40% @ 6.2 p/m; atrazine resistant 33% loss @ 5p/m hadss
A. arenicola	Sandhills Amaranth	N/A	In central states - wetland indicator	< 11% yield loss from 0,5 plants/m2		40% @ 6.2 p/m
A. blitoides	Prostrate Pigweed	N/A	In almost all states, weedy or invasive	< 11% yield loss from 0,5 plants/m2		40% @ 6.2 p/m
A. cruentus	Smooth Pigweed (cruentus)	N/A	Introduced and not really weedy in the states	< 11% yield loss from 0,5 plants/m2		40% @ 6.2 p/m
A. hybridus	Smooth Pigweed	0.25	Every state except Wyoming and Utah	< 11% yield loss from 0,5 plants/m2		40% @ 6.2 p/m
A. lividus	Livid Amaranth	0.02	Eastern seaboard	< 11% yield loss from 0,5 plants/m2		40% @ 6.2 p/m
A. palmeri	Palmer Amaranth	0.34	Southern states apart from Alabama and Indiana	11% yield loss from 0.5 plants p m		78% yield loss @ 8 plants p/m
A. powellii	Powell Amaranth	0.005	Everywhere except for Georgia, Alabama Tennessee and Kentucky	< 11% yield loss from 0,5 plants/m2		40% @ 6.2 p/m
A. quitensis	Pigweed (quitensis)	N/A	Not in states			40% @ 6.2 p/m
A. retroflexus	Redroot Pigweed	0.14	Everywhere	< 11% yield loss from 0,5 plants/m2		38% @ 8 plants
A. rudis	Common Waterhemp	3.84	Eastern states + Washington, Idaho and California	< 11% yield loss from 0,5 plants/m2		56% @ 8 plants p m
A. tuberculatus	Tall Waterhemp	0.04	Eastern states + Washington, Idaho and California			40% @ 6.2 p/m
Chenopodium album	Fat hen	1.05	All states	0 wwheat, 5% loss from 25 p/m Swt (UK)	35%loss @ 5 p/m hadss	28% @ 3.6 p/m; 38% loss @ 5p/m hadss
C. polyspermum	Manyseeded Goosefoot		All states			
Conyza canadensis	Horseweed	1.37	All states			0-30%
Fallopia convolvulus	Climbing Buckwheat		All states	4% loss @ 11.3 p/m-	10% loss @ 5 p/m hadss	15% yield loss@ 5 p/m
Galium aparine	Cleavers		All states	5% @ 2p/m		
Senecio vulgaris	Common Groundsel		All states	5%loss@84ppm		

Table 2. Biological characteristics of the main herbicide-resistant weed species in The USA.

Species	Common name	Mean number Seeds/plant	Crossing category	No. of flowering months
Amaranthus albus	Tumble Pigweed	50000		5
Amaranthus arenicola	Sandhills Amaranth		outcrossing	4
Amaranthus blitoides	Prostrate Pigweed	14600	self	7
Amaranthus cruentus	Smooth Pigweed (cruentus)	3500	mostly outcrossing	4
Amaranthus hybridus	Smooth Pigweed	100000	outcrossing	3
Amaranthus lividus	Livid Amaranth		mostly outcrossing	3
Amaranthus palmeri	Palmer Amaranth	250000	outcrossing	3
Amaranthus powellii	Powell Amaranth	5000		4
Amaranthus quitensis	Pigweed (quitensis)		self	
Amaranthus retroflexus	Redroot Pigweed	250000	mostly self	5
Amaranthus rudis	Common Waterhemp	250000	outcrossing	4
Amaranthus tuberculatus	Tall Waterhemp	100000	outcrossing	3
Atriplex patula	Spreading Orach	3050	mostly self	5
Chenopodium album	Lambsquarters, Fat hen	11500	outcrossing	3
Chenopodium polyspermum	Manyseeded Goosefoot	11500	outcrossing	4
Conyza canadensis	Horseweed	50000	Mostly self	5
Fallopia convolvulus	Climbing Buckwheat	6000	self	5
Galium aparine	Cleavers	350	outcrossing	2
Senecio vulgaris	Common Groundsel	5000	self	12
Papaver rhoeas	Common Poppy	20000	outcrossing	6
Stellaria media	Common Chickweed	2500	Mostly self	12

Table 3. The ecology of the main herbicide-resistant weed species in the USA.

Species	Common name	Germination period	Rate of growth	Dormancy	Crop type
Amaranthus albus	Tumble Pigweed	summer - earlier than waterhemp	Less fast than waterhemp		Corn & soya – spring crops
Amaranthus arenicola	Sandhills Amaranth	summer - earlier than waterhemp	Less fast than waterhemp		Corn & soya – spring crops
Amaranthus blitoides	Prostrate Pigweed	summer - earlier than waterhemp	Less fast than waterhemp		Corn & soya – spring crops
Amaranthus cruentus	Smooth Pigweed (cruentus)	summer - earlier than waterhemp	Less fast than waterhemp		Corn & soya – spring crops
Amaranthus hybridus	Smooth Pigweed	summer - earlier than waterhemp	Less fast than waterhemp		Corn & soya – spring crops
Amaranthus lividus	Livid Amaranth	summer - earlier than waterhemp	Less fast than waterhemp		Corn & soya – spring crops
Amaranthus palmeri	Palmer Amaranth	summer - earlier than waterhemp	Less fast than waterhemp biomass > redroot or albus		Corn & soya – spring crops
Amaranthus powellii	Powell Amaranth	summer - earlier than waterhemp	Less fast than waterhemp	50%	Corn & soya – spring crops sugar beet kale
Amaranthus quitensis	Pigweed (quitensis)	summer - earlier than waterhemp	Less fast than waterhemp		Corn & soya – spring crops
Amaranthus retroflexus	Redroot Pigweed	summer - earlier than waterhemp	Less fast than waterhemp		Corn & soya – spring crops
Amaranthus rudis	Common Waterhemp	middle to late growing season	Very fast		Corn & soya – spring crops
Amaranthus tuberculatus	Tall Waterhemp	middle to late growing season	Very fast		Corn & soya – spring crops
Chenopodium album	Fat hen	Spring - early season		70% dormancy 1st year	Mainly spring (soya, corn)
C. polyspermum	Many-seeded Goosefoot	Spring			4
Conyza canadensis	Horseweed	Winter (UK) Spring (USA)			soya
Fallopia convolvulus	Climbing Buckwheat	Spring and whole growing season when not drought	Quickly colonises bare ground & climbs crops	97% germination of these at high temp	Cereals other crops
Galium aparine	Cleavers	Autumn spring			2
Senecio vulgaris	Common Groundsel	Spring/autumn			Horticultural & cereal crops

APPENDIX 3

Geographic spread and herbicide resistance status

In order to begin to determine the proportion of land infested with reported resistant weeds in the USA, the area of arable land infested with resistant Amaranth species was calculated, and the areas of crops for each of the infested states summed, (Figure 1). The area of each state under arable cropping was gathered from the USDA statistics website for 2005-6. The area of herbicide resistant species in each US state was calculated from the ISHRW database, using the maximum areas of weed resistance cases reported; these areas are estimates of cropping areas infected when the resistance case was first reported. Notes on the areas where the weed species can be found were taken.

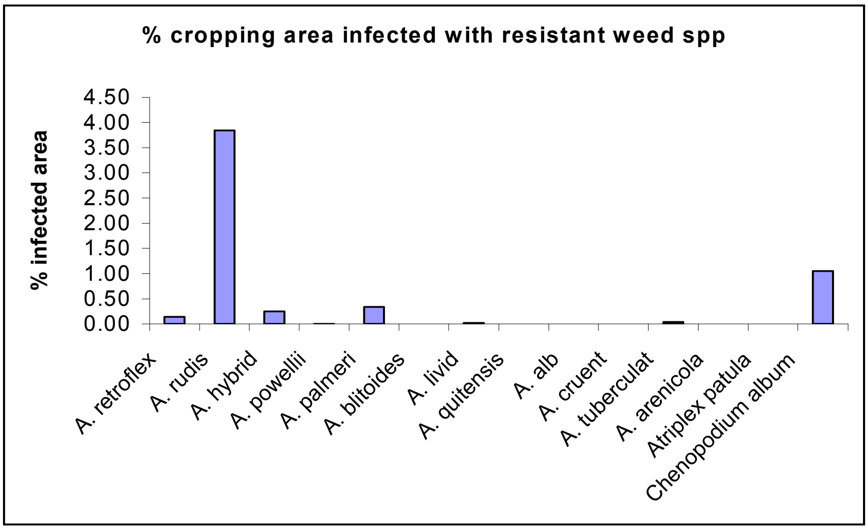
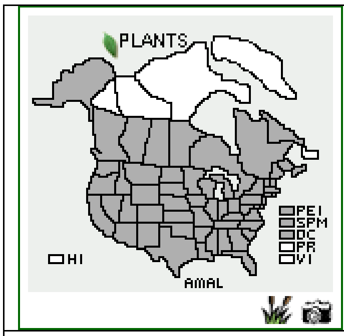
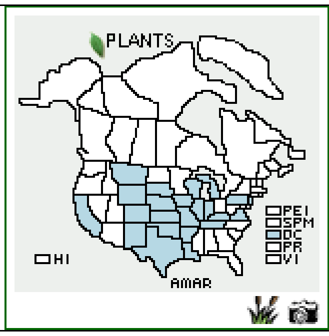
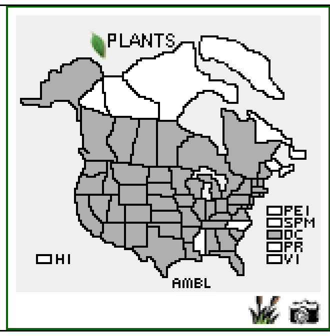
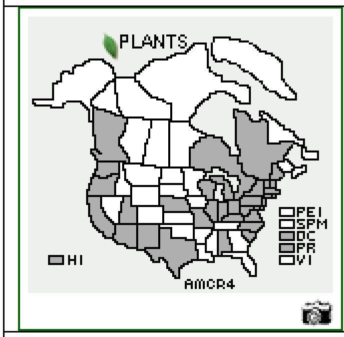
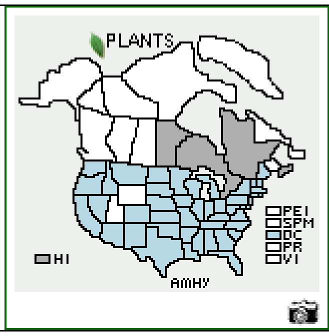
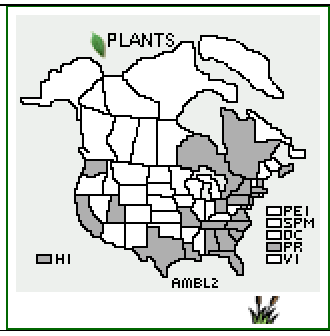
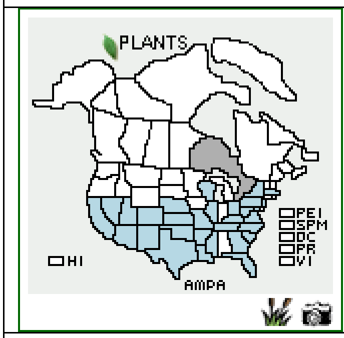
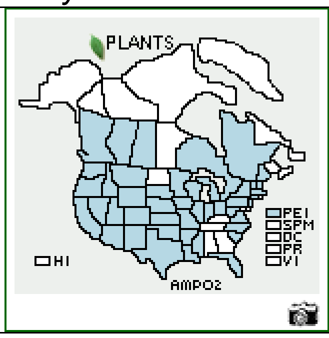
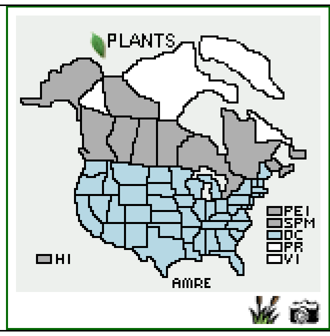
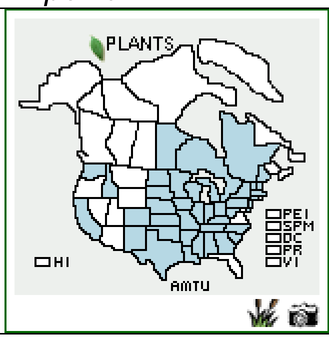


Figure 1. The percentage of cropped area infested with resistant weed species in the USA.

As much as 4% of the arable cropping area in states where the resistant weeds were found were infested with *A. rudis* while *A. retroflexus*, *A. hybridus*, and *A. palmeri* are also found in significant quantities. Some of the species are found in the same farms where for example *A. retroflexus* may show herbicide resistance while *A. rudis* may not (Bravo & Curran, 2001). *A. quitensis* is not found in the USA but is a major weed of soybean in South America.

APPENDIX 4

			
A. albus	*A. arenicola*	*A. blitoides*	
			
A. cruentus	*A. hybridus*	*A. lividus - blitum*	
			
A. palmeri	*A. powelli*	*A. retroflexus*	
			
	A. rudis and *A. tuberculatus*		

Key blue-native, grey introduced

Figure 1. Distribution maps of Amaranth species in the USA.