HERBICIDES AND PLANT PHYSIOLOGY

ANDREW H. COBB

THIRD EDITION

WILEY Blackwell

Herbicides and Plant Physiology

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Third Edition

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Preface

He who has bread may have many troubles; he who lacks it has only one.

(Byzantine proverb)

A peasant must stand for a long time on a hillside with his mouth open before a roast duck flies in.

(Chinese proverb)

The origin of the word herbicide is a combination of the Latin words *herba* (noun, herbaceous plant) and *caedere* (verb, to kill; R.L. Zimdhal, *Weed Science* **17**, 137–139, (1969).

It is now 30 years since the first edition of this book was published and so it is timely to reflect on herbicide use and the environmental consequences of their use. While we now have fewer products in our agrochemical armoury, farmers and growers have become dependent on fewer active ingredients, and glyphosate dominates the global market. This third edition aims to update the reader on how herbicides contribute to modern agriculture, how they are discovered and developed, and how they interact with plant growth and development and the environment. Since the publication of the second edition in 2010 there have been many advances in our understanding of plant physiology, especially regarding how plants function in tune with their ever-changing environment and how post-translational modifications provide regulatory control of most plant processes. Modern agriculture, however, still faces many challenges.

1 *The global food challenge*. To some, the continuing expansion of the human population will inevitably outstrip the growth of our food supply, resulting in global starvation. To others, an expansion of arable land, a growing global food trade and the increases in crop yield predict a more optimistic future. Yet is it inevitable that a growing food supply will continue to meet demand?
2 *The problem*. More than half the global population will suffer some form of malnutrition by 2030 unless urgent action is taken to increase access to food of high nutritional quality. The Food and Agriculture Organization of the United Nations (FAO *et al*., 2017) estimated that 815 million persons were hungry in 2016 (11% of the global population), an increase of 35 million since 2015. While 155 million children have stunted growth owing to poor nutrition, 2 billion persons suffer from hunger, while 1.9 billion adults and 41 million children are either overweight or obese. In addition, the human population is expected to grow by about 80 million per annum to an estimated 10 billion in 2050 (Oerke and Dehne, 2004). Furthermore, the global impact of the current covid-19

pandemic could result in at least a further 200 million undernourished persons. How can we expect to produce 70% more food to feed them all?

3 *Food security*. Food security is an increasing global problem in the face of climate change, combined with increasing populations and volatile food prices. With the global population growing at 230,000 persons each day and 60% of us now living in cities, the pressure on farmers to increase crop yields is ever present. At the same time, in the UK as an example, the land available per head of population has decreased from 0.8 to 0.2 hectares in the last 50 years. Every year 12 million hectares is degraded globally owing to drought, de-forestation and desertification, an area roughly the size of Nicaragua, the largest country in Central America. Furthermore, global freshwater supply is becoming increasingly limited and unreliable to an estimated 700,000 persons, notwithstanding the fluctuations in weather as a result of climate change. We are experiencing greater extremes of weather, such as flooding or drought, and so we need to use the available fresh- and artesian-water more wisely. This is especially so whether we grow crops or raise animals. For example, it is estimated that 70 litres of water are needed to produce one apple, whereas 15,000 litres are needed for one kg of beefsteak! It is interesting to note that the carbon footprint of beef and lamb is three times that of pork, five times that of chicken, over 30 times that of bread wheat and 50 times that of potatoes. Urbanisation and increasing incomes generate a higher demand for animal protein, yet beef production requires four times more land than dairy, per unit of protein consumed. In addition, beef is seven times more resource intensive than pork and poultry, and 20 times more so than pulses. Not forgetting that animal production results in increased greenhouse gas emissions. It is a further uncomfortable fact that about a third of all food produced never reaches the table. This value is higher for fruit and vegetables, and such losses are even higher in the developing world, owing to the lack of effective storage and/or transport (IFPRI, 2016).

As available land for farming is in ever shorter supply and extremes in climate become more evident, many scientists predict an increased degradation of soils and a need for increased attention to land management. In recent years in the UK, for example, farmers have seen above average rainfall with increasing soil erosion, degradation and run-off. Palmer and Smith (2013) noted that 75% of fields planted with maize or potatoes in the south-west of England were severely damaged by soil degradation, with one in five sites experiencing serious rill and gully erosion. Some 60% of fields growing winter cereal crops, such as wheat and barley also displayed high to severe soil degradation. Techniques to avoid soil compaction, such as topsoil lifting or sub-soiling, are options to loosen soil layers, but the use of increasingly large and heavy machinery increases the risk. These authors concluded that soils with good agricultural properties are over-exploited in crop production and, as a result, can become highly degraded. Conversely, chalk and limestone soils degrade less.

A further definitive study, by Challinor *et al*. (2016), has predicted that gradually rising temperatures in Africa, and more droughts and heatwaves caused by climate change, will have a profound impact on maize yields. Higher temperatures reduce the length of time between planting and harvesting, which results in less time to accumulate biomass and yield. They also predict similar shortening of time to yield for maize crops across the tropics and suggest that maize breeding systems must adapt to increasing temperatures to ensure positive yields in the decades ahead.

A further interesting area of research would be to investigate how the major weeds of maize crops may also adapt to increasing growth temperatures, with especial attention to weeds exhibiting C_4 photosynthesis.

4 *Greater intensification?* In a comprehensive and thought-provoking study, Fischer *et al*. (2014) concluded that greater crop yields are possible through a greater intensification of agriculture, especially in Sub-Saharan Africa. This assumes more agricultural research, development and training in the developing world and a more efficient use of inputs, such as plant protection products. What is certain is that global governments will need to invest substantially in agriculture to achieve the yield increases necessary to feed the world. Greater meat consumption and an expanding human population implies that crop productivity needs to double by 2050.

5 *Sustainability*. One widely used definition of sustainability is ‘meeting the needs of the present without compromising the ability of future generations to meet their own needs’ (DEFRA, UK). Another considers that ‘a sustainable agriculture is ecologically sound, economically viable and socially just and humane’ (Alliance for Sustainability, www.afors.org). How can humankind tackle climate change, reduce population growth, cut out waste, educate consumers in the developed world to eat less, conserve freshwater and eat more plant products and fewer animals? Political awareness, more education and an alert and informed media may provide the answer. Indeed, Ehrlich and Harte (2015) ‘urge policymakers around the world to move the issue of food security to the top of the political agenda’. And they conclude that ‘anything less is a recipe for disaster’.

6 *Can organic agriculture feed the world?* Regarding crop production, organic practices infer that the use of inorganic crop nutrition products is not allowed, genetically modified crop cultivars are not permitted and the use of chemical plant protection products for the control of pests, weeds and diseases is forbidden. Such practices are becoming widely accepted in the developed world, as they are seen as a more ‘natural’ means of crop production. Those that espouse organic farming practices often say that it is better for the environment, since it requires fewer inputs, but it is generally agreed that organic farming is less productive per hectare than conventional, intensive agriculture. More land would be needed for equivalent yields, and conversion to organic practice would release more organic carbon into the environment. Furthermore, it is doubtful that legume cover crops could replace the nitrogen fertiliser needed to give higher yields (Connor, 2008). Perhaps in the future, nitrogen fixation from the atmosphere will be possible using genetically engineered crop plants?

The EU Farm to Fork Strategy, launched on 20 May 2020, has ‘aspirational targets’ for 2030 for a 50% cut in pesticide use and a commitment to dedicating 25% of agricultural land to organic farming. One wonders if the consequences of reduced yields and higher prices, to name but two, have been thought through. Furthermore, the aspiration to replace pesticides with ‘biocontrol agents’ appears idealistic. Although regularly promoted, an agreed definition of biocontrol remains elusive and, at the present time, commercial agents are expensive, are unproven in the field and no viable weed biocontrol methodology exists. At a time of imminent global recession owing to the covid-19 pandemic, a global scarcity of food is predicted, made worse by plagues of locusts in Africa, Arabia, Iran and Pakistan adding to pressures on food security. Can food producers realistically promote organic agriculture and cut pesticide use in such uncertain times? Instead, can we use our existing practices more effectively?

7 *Plants for the future: genetic diversity*. In 2016, the Royal Botanic Gardens, Kew, UK, released a report on the state of the world's plants. It noted that an estimated 31,000 plant species have a documented use for medicines, food and materials. There are an estimated 391,000 vascular plants known to science of which 369,000 species are flowering plants. A further 2000 new vascular species are described each year. Many are wild relatives of known crops that can be a source of genetic variation to improve our crops in the future, such as tolerance to drought or possess a unique metabolism. Some 21% of the world's plants, however, are currently threatened with extinction, especially in declining rainforests. Humankind must preserve this genetic biodiversity in seed banks at all costs for future generations (www.stateoftheworldsplants.org). The human population derives 50% of its calorific intake from only three species, namely rice, wheat and maize. The rest is derived from only 20 species. Having so few staple crops means that we lack diversity in our diets and have an over-reliance on the chosen few. Can conventional plant breeding produce the advances in yield needed to feed our global population? Perhaps it can, with the application and more widespread adoption of gene editing techniques developed in the last decade.

8 *Can we survive without plant protection products?* Currently, global agriculture is heavily reliant on plant protection products, such as herbicides, plant growth regulators, fungicides and insecticides, to maximise crop yields. Without an equivalent process, yields would be reduced by at least 20–40%, so an increase in food prices would inevitably follow, with public unrest and food volatility. The reader is encouraged to note Oerke and Dehner (2004) and Pesticides in Perspective (n.d.) for further details.

I note with concern that the EU is planning to withdraw as many as 75 active ingredients from the crop protection armoury. In addition to yield losses, this will erode farmers' margins and reduce farm productivity across the EU, and over a million jobs are at risk of being lost. There are no current viable alternatives to the use of agrochemicals. Their judicious use should be promoted and these agents preserved if we are to feed the world and ensure future food security. In order for plant protection products to be used effectively, it is imperative to have an understanding of the biology of the target organisms and how an active ingredient works in both the plant and the environment. Thus, an understanding of weed biology, soil science and plant physiology underpins herbicide choice, use and effectiveness.

9 *Is science and technology the answer?* Scientists and technologists consider that appropriate scientific and technological developments might come to the rescue of humankind. Why such optimism? The answer lies in recent research findings reported in the plant sciences literature, some examples of which are noted below. The first reports a rice cultivar that has been engineered to have fewer stomata, which has resulted in an increased tolerance to drought and water availability, giving equivalent or increased rice yields. The importance of this finding is the knowledge that 2500 litres of water are typically required to produce 1 kg of rice. The authors consider that rice plants with fewer stomata should perform better when limitations on water supply threaten food security (Caine *et al*., 2018).

A second innovation is the use of gene editing to understand how plants are able to perceive and respond to environmental signals at the cellular level and respond by alterations in gene expression. In this way, plant scientists are able to understand how biotic and abiotic stimuli, such as responses to disease or environmental change, can alter growth, development and crop yield. This advance is largely due to the generation and testing of mutants that can be incorporated into plant breeding programmes. Examples include resistance to drought, resistance to salinity, temperature and water-logging, insect and disease resistance, potatoes free from late blight, enhanced concentrations of omega oils and vitamins, fruit and vegetables that do not turn brown on impact, and low-gluten wheat, to name but a few.

A third example is the RIPE project – Realising Increased Photosynthetic Efficiency – for sustainable increases in crop yield (www.ripe.illinois.edu). This is a collaboration of US, Australian, Chinese, German and UK universities that began in 2012 with an aim of increasing global agricultural production. Several research strategies have been developed with successful investigations that include:

- relaxing mechanisms of photoprotection;
- by-passing photorespiration;
- optimising enzyme activity in the photosynthetic carbon reduction cycle;
- increasing the efficiency of RuBisCo; and
- optimising canopies for photosynthesis.

Also of note the C4 Rice Project (www.c4rice.com) that is jointly funded by the Bill and Melinda Gates Foundation, in which researchers from seven institutions in five countries are working together to develop high-yielding rice cultivars. Their aim is to use gene editing to introduce C_4 photosynthetic machinery into rice, a C_3 crop, which currently accounts for 19% of all calories consumed in the world. If successful, rice plants could be 50% more productive.

10 Finally, the '*Hands Free Hectare*' project in the UK, demonstrated in 2016 that it is possible to drill, tend and harvest a crop of spring barley without operators of machines or agronomists in the field. It proves that there is no technical barrier to automated field agriculture. Weed control is achieved by aerial sensors that ensure that only weed-infested areas of a field are sprayed, rather than the whole field, thereby reducing inputs. It is assumed that unmanned automation will become an increasingly important part of agriculture in the future. Achieving precision spraying with dedicated robots fitted with associated sensors is a current engineering challenge (Ghaffarzadeh, 2017). Flavell (2016) has argued that we need to generate clear plans to increase the confidence of investors and society in the future of the plant sciences. Our collective challenge is therefore to see technological advances in the engineering and plant sciences lead to new concepts, products and innovations that will improve the efficiencies of agriculture in the future.

11 A key conclusion of the 2019 cross-sector review of weed management, commissioned by the UK Agriculture and Horticulture Development Board and the British Beet Research Organisation, was that the approach to Weed Management in the UK needs to be overhauled, and a major investment is required. The review noted that, *inter alia*: (a) essential information on weed management could be lost to the industry without appropriate key sources of references and an archive; (b) coordinated programmes of research and knowledge transfer are necessary to make the best use of depleted national funding; and (c) the plant protection industry needs to be more unified and strategic to maximise the chances of such methods and research results making an economic difference to farms and growers. I hope that the contribution of research institutes, colleges and

universities are to the fore in any future update in the training of the next generations of plant protection personnel.

12 As we have entered a new decade, agrochemical inputs are becoming increasingly under scrutiny and some would argue that agrochemical technology is reaching its limits (Altieri, 2019). Why is this?

- Large-scale crop monocultures occupy about 80% of the 1.5 billion hectares currently used in global agriculture.
- Approximately 2.3 billion kg of pesticides are applied each year to keep weeds, fungal and insect pests at bay.
- However, less than 1% of pesticides reach the target weed or pest, so that most ends up in the soil, water and the air, leading to declines in biodiversity, especially pollinators, and the natural enemies of pests.
- Monoculture agriculture leads to pesticide resistance.

It follows that the removal of pesticides and herbicides will restore biodiversity and a renewed interest in the biological control of pests. Biodiversity can also be enhanced using cover crops, inter-cropping, rotations, agroforestry and the introduction of livestock into crop fields. Surrounding these fields with hedgerows and corridors also generates more complex habitats, as field margins are reservoirs of the natural enemies of crop pests, and provide over-wintering sites for wildlife. In this way, it is thought that replacing monocultures with more complex agricultural systems will contribute to yield advantages via improved biodiversity, enhanced soil quality and resilience to climate change. Such arguments are ecologically persuasive, but more evidence, including detailed cost/benefit analysis, is required before extrapolation to weed control by herbicides. Nonetheless, the observed global increase in weed resistance to herbicides in recent decades is clearly linked to monoculture, and shows no signs of decline.

13 So how can politicians, growers, farmers and the agrochemical industry become more ecologically aware and promote more sustainable practices?

- The industry should recommend and use technologies for a more precise application of agrochemicals that will reduce application volumes and cumulative dosage.
- Greenhouse gas emissions can be reduced and soils preserved by promoting minimal tillage and fewer, but more targeted agrochemical applications.
- More informed farming practices that are sustainable for the use of agrochemicals should be encouraged by continuing professional development and re-education of farmers and growers.
- Biodiversity should be encouraged by returning to more complex agro-ecosystems.

We have the tools and knowledge to defeat hunger and malnutrition, but do we have the political will and commitment to do so?

Despite these reservations it is important to remember that without herbicides and the sustainable intensification of agriculture we would not be able to feed the existing and growing global population. We must remain alert, however, to the environmental consequences of their use. Furthermore, it is vital that independent research in the plant sciences continues to be supported by national bodies in universities and research institutes. New discoveries and current understanding of how plants are adapted to their ever-changing environments will continue to drive agrochemical research and development in the years to come.

The starting point of this book is weed biology. Subsequent chapters consider the modern plant protection products industry, how herbicides are discovered and developed, how they gain entry into the plant and move to their sites of action, and the basis of herbicide selectivity. Detailed and updated accounts follow of how herbicides interact with the major physiological processes in plants, leading to weed control. This begins with the inhibition of photosynthesis, followed by pigment biosynthesis, interactions with the plant growth regulator, auxin, lipid biosynthesis, amino acid biosynthesis, cell division, cellulose biosynthesis, the plant kinome, herbicide resistance, the development of genetically modified herbicide-resistant crops and a consideration of some new targets for the future development of new herbicides.

In the dozen years since the last edition was written, there have been many advances reported in the plant physiology literature. There has been continuing progress in our understanding of the *Arabidopsis* genome and our model plant species, and gene editing techniques are now commonplace. It is fascinating to recall that 10 years ago gene editing techniques had not been published. We now understand more about the mechanisms whereby environmental change and protein synthesis are in tune with both biotic and non-biotic stresses, enabling plant physiology to adapt to an ever-changing plant environment. Consequently, much of this text is new and many recent references have been added. Note, however, that many older references and figures have been retained because they remain relevant in demonstrating how our understanding has developed, and that the work of previous generations of plant scientists is not forgotten. Of course, the errors are still mine and hopefully will be remedied in time.

It is with regret that the co-author of the second edition of this book, Dr John Reade, has been unable to contribute to this volume, owing to other commitments. He continues to teach the next generations of plant scientists at Harper Adams University and supervises research students with his trademark enthusiasm and intelligence.

And finally,

I think it must be rather nice
to live by giving good advice;
to talk of what the garden needs
instead of pulling up the weeds. (Reginald Arkell, 1882-1959)

Andy Cobb
July 2021

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Chapter 1
An Introduction to Weed Biology

> One year's seed is seven year's weed.
>
> A traditional rhyme

1.1 Introduction

The human race has been farming for over 10,000 years. Weeds have been an unwelcome presence alongside crops ever since the first farmers saved and planted seeds in the region that is now present-day Turkey and the Middle East. Indeed, when these early farmers noticed a different plant growing, decided they did not want it and pulled it up, they were carrying out a form a weed control that is still used today: hand roguing.

But what are weeds? Weeds are all things to all people, depending on the viewpoint of the individual. To some they are plants growing where they are not wanted; to others they are plants growing in the wrong place, in the wrong quantity, at the wrong time; and to some they are regarded as plants whose virtues have yet to be fully discovered! The need to control weeds only arises when they interfere with the use of the land, and this is usually in the presence of a crop, such as in agriculture and horticulture. Weed control may also be necessary in other situations including amenity areas, such as parks and lawns, in water courses, or on paths and drives where the presence of plants may be regarded as unsightly. It should not be overlooked, however, that weeds contribute to the biodiversity of ecosystems and should only be removed when financial or practical implications make their presence unacceptable. With this in mind an appropriate definition of a weed is:

> Any plant adapted to man-made habitats and causing interference of the use of those habitats. (Lampkin, 1990)

Or

> A plant whose virtues remain to be discovered. (Emerson, 1912, see https://theysaidso.com/quote/ralph-waldo-emerson-what-is-a-weed-a-plant-whose-virtues-have-never-been-discovered)

Herbicides and Plant Physiology, Third Edition. Andrew H. Cobb.

1.2 Distribution

On a global basis only about 250 species are sufficiently troublesome to be termed weeds, representing approximately 0.1% of the world's flora. Of these, 70% are found in 12 families, 40% alone being members of the Gramineae and Compositae. Interestingly, 12 crops from five families provide 75% of the world's food and the same five families provide many of the worst weeds (Table 1.1). This implies that our major crops and weeds share certain characteristics and perhaps common origins.

Table 1.1 Important plant families which contain both the major crops and the worst weeds of the world.

Number of species classified as the world's worst weeds (%)	Family	Examples of major crops	Examples of major weeds	Common name
44	Gramineae	Barley, maize, millett, oats, rice, sorghum, sugar cane and wheat	*Elytrigia repens* (L.)	Couch
			Alopecurus myosuroides (L.)	Black-grass
			Avena fatua (L.)	Wild oat
			Sorghum halepense (L.) Pers.	Johnson grass
			Echinochloa crusgalli (L.)	Barnyard grass
4	Solanaceae	White potato	*Solanum nigrum* (L.)	Black nightshade
			Datura stramonium (L.)	Jimsonweed
			Hyoscyamus niger (L.)	Henbane
5	Convolvulaceae	Sweet potato	*Convolvulus arvensis* (L.)	Field bindweed
			Cuscuta pentagona (Engelm)	Field dodder
			Ipomoea purpurea (L.) Roth	Tall morning glory
5	Euphorbiaceae	Cassava	*Euphorbia maculata* (L.)	Spotted spurge
			Euphorbia helioscopia (L.)	Sun spurge
			Mercurialis annua (L.)	Annual mercury
6	Leguminosae	Soybean	*Cassia obtusifolia* (L.)	Sicklepod
			Melilotus alba (Desc)	White sweetclover
			Trifolium repens (L.)	White clover

Source: Radosevich, S.R. and Holt, J.S. (1984) *Weed Ecology: Implications for Vegetation Management*. New York: Wiley. Reproduced with permission of John Wiley & Sons.

1.3 The importance of weeds

Most plants grow in communities consisting of many individuals. If the resources available (such as space, water, nutrients and light) become limiting then each species will be forced to compete. Weeds are often naturally adapted to a given environment and so may grow faster than the crop, especially since the crop species has been selected primarily for high yield rather than competitive ability. A unit of land may therefore be regarded as having a finite potential biomass to be shared between crop and weeds, the final proportion being determined by their relative competitive ability.

1.4 Problems caused by weeds

The most obvious problem caused by weeds is the reduction of yield through direct competition for light, space, nutrients and water. Weeds can have many further effects on the use of land, as illustrated in Table 1.2.

Table 1.2 Problems caused by weeds.

Problem	Mechanism
Reduced crop yield	Interference with access to light, water and nutrients
Reduced crop quality	Admixture of contaminating seeds in arable crops
	Contamination of vegetable crops
Delayed harvesting	Conservation of moisture may delay ripening and increase moisture level when harvested
Interference with harvesting	Climbing plants making combining more difficult
	Vigorous, late-growing weeds interfering with harvesting of potatoes and sugar beet
Interference with animal feeding	Plants with spines or thorns inhibiting animal foraging
Poisoning	Poisoning either through ingestion or through contact
Tainted animal products	Imparting an undesirable flavour, e.g. to milk
Plant parasitism	Competing for nutrients and water
Reduced crop health	Acting as an alternative host for crop pests and diseases
	Increasing the amount of vegetation at the base of the crop, increasing moisture and disease
Reduced animal (and human) health	Acting as an intermediate host or a vehicle for ingestion of pests and parasites
	Photosensitivity
	Teratogens
	Carcinogens
Safety hazard	Reducing vision on roadsides
	Causing a risk of fire under electricity lines and on garage forecourts
Reduced wool quality	Hooked seeds reducing the value of fleece
Water flow prevented	Plant mass blocking ditches and irrigation channels
Allelopathy	Releasing substances toxic to the growth of crop plants
Impacted crop establishment	Vegetation preventing the establishment of young trees
	Competing for space with establishing crops

Source: Naylor, R.E.L. and Lutman, P.J. (2002) What is a weed? In: Naylor, R.E.L. (ed.) *Weed Management* Handbook, 9th edn. Oxford: Blackwell Publishing/BCPC. Reproduced with permission of John Wiley & Sons.

1.4.1 Yield losses

Crop losses approaching 100% are recorded in the literature (Table 1.3; Lacey, 1985). Such yield losses will, of course have a profound effect on a national economy in terms of both the need to import foodstuffs and the costs of weed control. Despite the many methods of weed management that are now available worldwide, it is estimated that approximately 13% of crop losses are still due to weeds alone (Table 1.4). Indeed, in 1974 the annual cost of weeds to agriculture in the USA was estimated at US$10 billion, with 50% owing to yield reductions and 50% owing to the cost of weed control (Rodgers, 1978).

In the tropics, parasitic weed species from the genera *Cuscuta* (dodders), *Orobranche* (broomrapes) and *Striga* (witchweeds) can have a profound effect on a range of crops. They absorb nutrients directly from the crop plant, which may not set seed at all in the case of cereals such as sorghum.

Weed control techniques are therefore aimed at the reduction in the competitive ability of weeds in a crop and the prevention of weed problems in a future crop. The former is increasingly based on chemical use, and the latter also requires suitable cultural and agronomic practices.

Yield loss may be usefully related to the number of weeds per unit area causing a defined yield loss in a defined crop, that is, as a Weed Threshold (Table 1.5) or as a Crop Equivalent

Table 1.3 Examples of yield losses owing to weeds.

Crop	Yield loss (%)	Country
Cassava	92	Venezuela
Cotton	90	Sudan
Groundnuts	60–90	Sudan
Onions	99	UK
Rice	30–73	Colombia
Sorghum	50–70	Tanzania/Nigeria
Sugar beet	78–93	Texas, USA
Sweet potatoes	78	West Indies
Wheat*	66	UK
Yams	72	Nigeria

Source: Lacey, A.J. (1985) Weed control. In: Haskell, P.T. (ed.) *Pesticide Application: Principles and Practice*. Oxford: Oxford University Press, pp. 456–485. Reproduced with permission of Oxford University Press.
* From Moss (1987).

Table 1.4 Estimated percentage crop losses owing to weeds, 1988–90 (from Oerke *et al.*, 1995).

	Estimated loss owing to weeds (%)
Africa	16.5
North America	11.4
Latin America	13.4
Asia	14.2
Europe	8.3
Former Soviet Union	13.0
Oceania	9.6
Average	**13.1**

Source: Oerke, E.C., Dehne, H.W., Schonbeck, F. and Weber, A. (eds) (1995) *Crop Production and Crop Protection: Estimated Losses in Major Food and Cash Crops*. Amsterdam: Elsevier.

Table 1.5 Relative competitive abilities of a number of common weeds found in winter cereals.

Weed species	5% yield loss (plants m^{-2})	Weed species	5% yield loss (plants m^{-2})
Galium aparine	1.7	*Poa annua*	50.0
Anisantha sterilis	5.0	*Epilobium* spp.	50.0
Avena fatua	5.0	*Polygonum aviculare*	50.0
Lolium multiflorum	8.3	*Sonchus* spp.	50.0
Alopecurus myosuroides	12.5	*Taraxacum officinale*	50.0
Brassica napus	12.5	*Fumaria officinalis*	62.5
Sinapis arvensis	12.5	*Geranium* spp.	62.5
Tripleurospermum inodorum	12.5	*Lamium purpureum*	62.5
Cirsium spp.	16.7	*Ranunculus* spp.	62.5
Convolvulus arvensis	16.7	*Veronica* spp.	62.5
Fallopia convolvulus	16.7	*Aethusa cynapium*	83.3
Papaver spp.	16.7	*Senecio vulgaris*	83.3
Chenopodium album	25.0	*Anagallis arvensis*	100.0
Myosotis arvensis	25.0	*Allium vineale*	250.0
Persicaria maculosa	25.0	*Aphanes arvensis*	250.0
Silene vulgaris	25.0	*Legousia hybrida*	250.0
Stellaria media	25.0	*Viola arvensis*	250.0

Source: Lutman, P.J., Boatman, N.D, Brown V.K. and Marshall, E.J.P. (2003) Weeds: their impact and value in arable ecosystems. In: *The Proceedings of the BCPC International Congress: Crop Science and Technology 2003* **1**, 219–226.

(the amount of resource an individual weed uses expressed as the number of crop plants this resource would support, although in practice it is the biomass of the weed and the crop which is measured). Generally, these figures have only been determined for weed interaction with major crops, but they give a good indication of the ability of a particular species to compete with all crops.

Yield loss may also occur in addition to direct competition for resources. Allelopathy is the production of allelopathic chemicals by one plant species that may inhibit (or, in the case of positive allelopathy, stimulate) the growth of other species. Anecdotal evidence of negative allelopathic effects has been reported for a number of weed species, although supporting research is often lacking. Recent findings have been reviewed by Olofdotter and Mallik (2001) and others (see *Agronomy Journal* vol. 93). Given the ample evidence of allelopathy exhibited by crop species, it is highly likely that many weed species will also display these effects, and that it is only a matter of time before research demonstrating this becomes readily available.

Further examples of yield loss caused by weeds include the effects on non-plant organisms. One example of this is the presence of dandelion (*Taraxacum officinale*) in fruit orchards. Dandelion flowers are preferentially visited by insect pollinators and so pollination of fruit blossom (and therefore fruit yield) is reduced.

1.4.2 Interference with crop management and handling

Some weeds can make the operation of agricultural machinery more difficult, more costly, or even impossible. The presence of weeds within a crop may necessitate the need for extra cultivations to be introduced. This often leads to crop damage, reduced yields and increased pest and disease occurrence, although in sugar beet crops, where inter-row cultivation is often carried out and has previously been associated with yield loss, recent findings suggest that careful implementation can result in no loss of root yield or sucrose content (Dexter *et al*., 1999; Wilson and Smith, 1999). This is possibly due to the development of tillage equipment that carries out more shallow cultivation and that is more carefully implemented, resulting in less seedling and root damage. Weeds can also affect the processes carried out prior to crop planting. For example, fat hen stems and leaves block the mesh of de-stoners, which are used prior to potato and other root crop planting. Species with rough, wiry stems that spread close to the ground (e.g. knotgrass, *Polygonum aviculare*) or are more erect in growth habit (e.g. fat hen, *Chenopodium album*) present major problems for the mechanical harvesting of many crops and can result in damage to machinery (e.g. pea viners) and subsequent harvesting delays. Other species can be troublesome when the crops are harvested by hand, such as the small nettle (*Urtica urens*) in strawberries and field bindweed (*Convolvulus arvensis*) in blackcurrants. The result is that fruit is not harvested and spoils on the plant.

1.4.3 Reduction in crop quality

Competition between crop and weed species can result in spindly leaf crops and deformed root crops which are less attractive to consumers and processors. A crop may have to be rejected if it contains weed seeds, especially when the crop is grown for seed, such as barley and wheat, and if the weed seeds are similar in size and shape to the crop, e.g. wild oats (*Avena fatua*) in cereal crops. Similar problems are encountered in the contamination of oilseed rape seed with seeds of weed species such as cleavers (*Galium aparine*). Where a proportion of the seed is saved for planting in subsequent seasons, this can cause a large increase in weed infestation. Contamination by poisonous seeds, such as darnel (*Lolium temulentum*) and corncockle (*Agrostemma githago*) in flour-forming cereals is also unacceptable and once led to vastly increased costs of crop cleaning. Such cleaning, however, has meant that these weeds are now probably extinct in agroecosystems in the UK. A further example that still causes major problems is black nightshade fruit (*Solanum nigrum*) in pea crops (Hill, 1977). In this case, the poisonous weed berry is of similar size and shape to the crop and so must be eradicated. Although grazing animals avoid poisonous species in pasture (e.g. common ragwort, *Senecio jacobea*), they may be difficult to avoid in hay and silage, and some species, notably the wild onion (*Allium vineale*), can cause unacceptable flavours in milk and meat.

1.4.4 Weeds as reservoirs for pests and diseases

Weeds, as examples of wild plants, form a part of a community of organisms in a given area. Consequently, they are food sources for some animals and are themselves susceptible to many pests and diseases. Because of their close association with crops, they may serve as important reservoirs or carriers of pests and pathogens, as exemplified in Table 1.6. Even where crop infestation does not occur, the presence of disease in weeds may cause problems, as is the case where grass weeds are infected with ergot (*Claviceps purpurea*), causing contamination of harvested grain with highly toxic ergot fragments.

Weeds may act as ‘green bridges’ for crop diseases, carrying the disease from one crop to another that is subsequently sown. Volunteer crops are particularly problematic in this

Table 1.6 Some examples of weeds as hosts for crop pests and diseases.

Pathogen or pest		Weed		Crop
1. Fungi				
Claviceps purpurea	(ergot)	Black-grass	*(Alopecurus myosuroides*)	Wheat
Gaeumannomyces graminis	(take-all)	Couch *(Elytrigia repens)*	Cereals	
Plasmodiophora brassicae	(clubroot)	Many crucifers		Brassicas
2. Viruses				
Tobacco ringspot		Dandelion	(*Taraxacum officinale*)	Tobacco
Cucumber mosaic		Chickweed	(*Stellaria media*)	Many crops
3. Nematodes				
Ditylenchus dipsaci	(eelworm)	Chickweed Spurrey	(*Stellaria media*) (*Spergula arvensis*)	Many crops
4. Insects				
Aphis fabae	(black bean aphid)	Fat hen	(*Chenopodium album*)	Broad and field beans

Source: Hill, T.A. (1977) *The Biology of Weeds*. London: Edward Arnold.

case and can, in severe cases, negate the use of break crops as a cultural control measure for diseases. In addition, weeds can provide over-wintering habitats for crop pests, resulting in quicker crop infestation in the spring. Ground cover provided by weeds can increase problems with slugs and with rodents, as the weeds provide greater cover and therefore reduced predation.

In 1994 and 1995 there were several severe outbreaks of the disease brown rot in potato in several European countries, especially in The Netherlands, which was possibly exported to other countries via infected seed potatoes. This extremely virulent pathogen (*Pseudomonas solanacearum*, syn. *Burkholderia solanacearum*, syn. *Ralstonia solanacearum*) causes a vascular ring rot in the developing tuber and causes a major loss of yield. Although often considered a soil-borne organism, it was not found to persist for long periods in the soil following the harvest of infected crops. However, it was found to survive in the aquatic roots of infected woody nightshade (*Solanum dulcamara*) growing at the edge of irrigation channels. Thus, it may be the case that the pathogen overwinters in this wild host and is leaching into watercourses used to irrigate the crop, thus spreading the disease. This perennial plant is now being eradicated from potato-growing areas. Several other species could also act as alternative hosts to the pathogen, including *Solanum nigrum* and *Tusilago farfara*, but further work is needed to confirm this.

1.5 Biology of weeds

Knowledge of the biology of a weed species is essential to the design of management strategies for that weed. An understanding of the life cycle of a species can be exploited in order to identify vulnerable times when weed management and control might prove more successful.

1.5.1 Growth strategies

According to Grime (1979), the amount of plant material in a given area is determined by two principal external factors, namely stress and disturbance. Stress phenomena include any factors that limit productivity, such as light, nutrient or water availability; and disturbance implies a reduction in biomass by factors such as cultivation, mowing or grazing. The intensity of both stress and disturbance can vary widely, with four possible combinations. However, only three growth strategies have evolved, as shown in Table 1.7. Although plants are unable to survive both highly stressed and disturbed environments, the other strategies have major significance to weed success.

Ruderals are the most successful agricultural weeds. These plants have typically rapid growth rates and devote most of their resources to reproduction. Because they inhabit recently disturbed environments there is little competition with other plants for resources, which therefore can be obtained without difficulty. They are generally short-lived ephemeral annuals that occupy the earliest phases of succession. Conversely, biennial and perennial weeds often employ a more competitive growth strategy in relatively undisturbed conditions. They use their resources perhaps less for seed production and more for support tissues, for example, to provide additional height for the interception of light, or more extensive root systems to obtain more water and minerals. Rapid growth rate may still be evident with high rates of leaf turnover. The third growth strategy, exhibited by the stress tolerators, is to reduce resource allocation to vegetative growth and seed production, so that the survival of relatively mature individuals is ensured in high-stress conditions. Consequently, they have slow growth rates and are commonly found in unproductive environments.

Many arable weeds have characteristics common to both competitors and ruderals, and are referred to as competitive ruderals. Indeed, most of the annuals listed in *The World's Worst Weeds* (Radosevich and Holt, 1984) fit into this category, and are found in productive sites where occasional disturbance is expected. Examples include arable land that is cultivated, and meadows and grassland that are grazed or mowed. Interestingly, most crop plants also adopt a competitive ruderal strategy with their rapid growth rates and relatively large seed production. Competition between crop and weed is then related to their relative abilities to exploit the resources available.

The practice of growing crops in monoculture has exerted a considerable selection pressure in the evolution of weeds. Many characteristics have evolved that contribute to weed success and the main ones are listed in Table 1.8. Fortunately, not all of these features are present in any one weed species, yet each character may give the weed a profound competitive advantage in a given situation. Some of these characteristics are discussed in more detail in the following sections of this chapter.

Table 1.7 Growth strategies of plants.

	Intensity of stress	
Intensity of disturbance	High	Low
High	Death	Ruderals
Low	Stress tolerators	Competitors

Source: Hill, T.A. (1977) *The Biology of Weeds*. London: Edward Arnold.

Table 1.8 The 'successful' weed.

Characteristic	Example species
1. Seed germination requirements fulfilled in many environments	*Senecio vulgaris*
2. Discontinuous germination (through internal dormancy mechanisms) and considerable longevity of seed	*Papaver* spp.
3. Rapid growth through the vegetative phase to flowering	*Cardamine hirsuta*
4. 'Seed' production in a wide variety of environmental conditions	*Poa annua*
5. Continuous seed production for as long as conditions for growth permit	*Urtica urens*
6. Very high 'seed' output in favourable environmental conditions	*Chenopodium album*
7. Self-compatible but not completely self-pollinating	*Alopecurus myosuroides*
8. Possession of traits for short- and long-distance seed dispersal	*Galium aparine*
9. When cross-pollinated, unspecialised pollinator visitors or wind pollinated	*Grass weeds in general*
10. If a clonal species, has vigorous vegetative growth and regeneration from fragments	*Cirsium arvense*
11. If a clonal species, has brittleness of leafy parts ensuring survival of main plant	*Taraxacum officinale*
12. Shows strong inter-specific competition by special mechanisms (e.g. allelopathic chemicals)	*Elytrigia repens*
13. Demonstrates resistance to herbicides through a number of resistance mechanisms	*Alopecurus myosuroides*

Source: Adapted from Baker, H.G. and Stebbins, G.L. (1965) *The Genetics of Colonising Species*. New York: Academic Press.

Invasive species have received far greater research focus in recent years (see, for instance, Shaw and Tanner, 2008 for a review), and DAISIE (Delivering Alien Invasive Species Inventories for Europe) currently reports 10,822 invasive species in Europe (this figure is for all invasive species, not just plants). Alien species present a real threat to biodiversity, and a number of political drivers have been put into place to combat their spread and reduce the occurrence of a number of alien species, including plants. These measures include the Convention of Biodiversity and the EU 2010 Halting Biodiversity Loss, both of which identify invasive weeds as being a key factor in biodiversity loss.

Most non-native plants in the UK were introduced by plant collectors in the last 200 years. They become invasive when they have negative impacts on native species, our economy and even our health. Alien plant species become a problem because they are growing in habitats away from their natural predators and so can spread with ease and do not need to invest valuable energy in biologically expensive chemical defence mechanisms. In addition, the Novel Weapons Hypothesis proposes that in some cases allelopathic chemicals produced by alien species are more effective against native species in invaded areas than they are against species from the alien's natural habitat (Inderjit *et al*., 2007). This gives further ecological advantage to some invasive species of plant.

The Royal Horticultural Society notes 1402 invasive plants in the UK, of which 108 can have negative effects, and its website offers advice and guidance on how they should be dealt with (www.rhs.org.uk/advice/profile?PID=530). The EU Regulation on Invasive Alien Species lists 36 plants.

Observations of the pathogens and predators that affect these invasive plants in their natural habitats may identify mycoherbicides and other biological controls that may prove useful in their management. Research into such controls for Japanese Knotweed (*Fallopia japonica*), Himalayan Balsam (*Impatiens glandulifera*) and Giant Hogweed (*Heracleum mantegazzianum*) have so far produced, at best, limited success (Tanner, 2008).

Moles *et al*. (2008) have recently proposed a framework for predicting plant species which may present a risk of becoming invasive weeds. This may prove more useful than Table 1.8 in risk assessment relating to alien species, prior to their becoming major weed problems.

1.5.2 Germination time

The success of some weeds is due to close similarity with a crop. If both the weed and the crop have evolved with the same agronomic or environmental conditions they may share identical life cycles and life styles. Thus, if weed seed maturation coincides with the crop harvest, the chances of weed seed spread are increased. This phenomenon is often apparent in the grasses, such as barnyard grass (*Echinochloa crus-galli*) in rice, and wild oat (*Avena* spp.) in cereals. In Europe, spring wild oats (*A. fatua*) germinate mainly between March and May, and the winter wild oat (*Avena ludoviciana*) shows maximum germination in November. Hence, the date of cereal sowing in relation to wild oat emergence is crucial to weed control. In general, weeds may be considered to occupy one of three categories: autumn germinators, spring germinators and those that germinate throughout the year. Figure 1.1 illustrates the germination patterns for a number of common arable weeds. Autumn-sown crops are more at risk from weeds that germinate during the autumn, when the crop is relatively small and uncompetitive. Conversely, weeds that cause problems in spring crops tend to be spring germinators (including the troublesome polygonums). Knowledge of the germination patterns of weeds plays a very important role in the designing of specific weed management strategies that will disrupt conditions conducive to the survival of the weed.

Further major problems are evident in sorghum, radish and sugar beet crops. Hybridisation of cultivated *Sorghum bicolor* (L.) Moench with the weed *S. halepense* (L.) Pers. results in an aggressive perennial weed that produces few seeds, but demonstrates vigorous vegetative growth. Similarly, hybridisation between the radish (*Raphanus sativus* L.) and the weed *R. raphanistrum* (L.) has produced a weedy form of *R. sativus* with dormant seeds and a root system that is more branched and penetrating than the crop. Lastly, hybridisation of sugar beet (*Beta vulgaris* (L.) subsp. *maritima*) has created an annual weed-beet that sets seed, but fails to produce the typically large storage root. In each of these examples of crop mimicry by weeds, chemical weed control is extremely difficult owing to the morphological and physiological similarities between the weed and the crop.

1.5.3 Germination depth

Most arable weeds germinate in the top 5 cm of soil and this is the region that soil-acting (residual) herbicides aim to protect. Where minimum cultivation or direct drilling is carried out, the aim is to avoid disruption of this top region of soil in an attempt to minimise weed-seed germination. A small number weed species can germinate from greater depths and this may be due to these species possessing larger seed. A good example of this is wild oat (*Avena* spp.), which can successfully germinate and establish from depths as low as 25 cm.