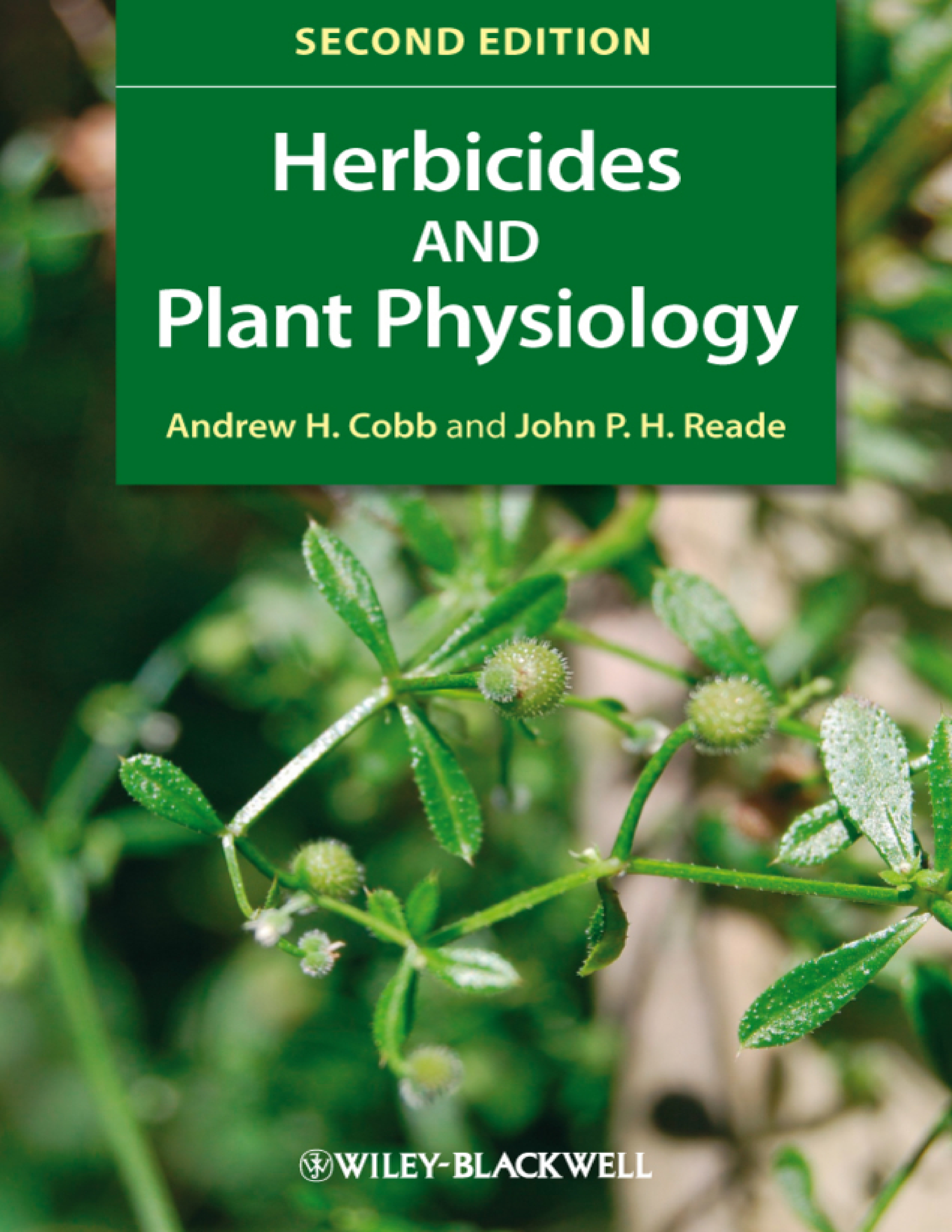
SECOND EDITION

Herbicides AND Plant Physiology

Andrew H. Cobb and John P. H. Reade



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Herbicides and Plant Physiology

Second Edition

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Preface

Whilst recently acting in the capacity of External Examiner at a UK Higher Education Institution, AHC encountered the following question on an examination paper:

> "Discuss why, after 50 years of using herbicides, weeds are still a major problem in agroecosystems."

The short answer, of course, is that the "weed problem" will never go away as long as crops are grown and harvested. The grower needs to be forever vigilant of the changing weed spectrum and of the need to use the appropriate methods available to ensure adequate control, including both crop and chemical rotation. The theory then is relatively simple, but in practice the grower is put under increasing pressure by variable returns, to repeatedly grow monocultures and rely on the cheapest methods of weed control and chemical inputs available. Too often a farmer will adopt a wait and see approach and then resort to a fire-fighting, last-m inute strategy for weed control.

Variable returns and environmental considerations are indeed forcing the farmer to reexamine the need for all chemical inputs, including fertilisers and crop protection agents. This will reduce costs but with a consequence of lower yields and reduced crop quality. On the other hand, a more judicious, measured use of agrochemicals at an appropriate dose may provide the most cost effective management of a weed problem. To do this, the farmer must know the land, understand its previous history of cropping and have good records of the previous usage of crop protection chemistry. Even then, as we develop new cropping practices, such as minimum cultivation or even organic farming, we can expect the weed population and spectrum to change, population density to alter and different species to gain prominence. These all create new and demanding challenges to weed management and control strategies.

Our starting point then, in a study of herbicides, must be to understand weed biology and the competing demands of weeds and crops. Only then is reflection possible to choose the most appropriate herbicide for the weed issue in question.

Subsequent chapters include considerations of how herbicides have been discovered and developed (Chapter 2), how they gain entry into plants and move to their site of action (Chapter 3), and the basis for herbicide selectivity (Chapter 4). Detailed accounts are then given of how herbicides interact with the major physiological processes in plants leading to plant death. This begins with the inhibition of photosynthesis (Chapter 5), followed by pigment biosynthesis (Chapter 6), interactions with the plant growth regulator, auxin (Chapter 7), lipid biosynthesis (Chapter 8), amino acid biosynthesis (Chapter 9), cell division (Chapter 10) and cellulose biosynthesis (Chapter 11). Chapter 12 gives a detailed and up to date presentation on herbicide resistance, leading to an account of the development and underlying science of herbicide tolerant crops (Chapter 13). Finally, Chapter 14 highlights further targets for herbicide development that may yield new products in the following decade(s).

In reviewing literature for this second edition, it may be tempting at a superficial level to believe that there is little new to report in this discipline since the first edition was published in 1992. Indeed, superficially, there are few novel modes of action to report with little exploitation of new target sites. A more detailed scrutiny, however, reveals the development of new triazine inhibitors of PSII (p 98), of the HPPD inhibitors (p 128), more clarity on the mode of action of the chloroacetamides (p 167) and the discovery of a new class of microtubule inhibitors (p 205) and inhibitors of cellulose biosynthesis (p 213) to name but five. Why have there been fewer herbicide discoveries in the recent years? Two main contributory factors come to mind. The first is the increasing costs to develop a new product that satisfies all the regulatory requirements. The second lies in the use of molecular approaches to induce herbicide tolerance into crops, thereby extending the usage of existing products. These areas are considered further in Chapters 2 and 13, respectively. Our understanding of the metabolism, environmental impact, genetics and molecular biology of herbicide action, particularly in relation to resistance, has also greatly improved. Indeed, this understanding has led to lower doses of new agrochemicals that are more effective than previous versions and are more environmentally benign. Furthermore, new methods have been established for high-throughput screening (p 38) to discover new agrochemicals.

Since the first edition of this book our understanding of plant physiology and metabolism in general has improved, especially utilising our knowledge of the *Arabidopsis* genome. This has generated potential for new target sites that may yield the new herbicides of the coming decades.

The need for crop protection agents remains essential, as eloquently summarised by Len Copping (2001).

“In the time it takes to read this sentence, another 20 people will have been added to the world’ s population. And by this time next week, enough people will have been born to establish a new city about the size of Birmingham in the UK or Detroit in the US. This rapid expansion is forecast to stabilise by 2050 at 11 billion, a 100% increase from 1998. Enormous sociological and economic progress must occur to allow such increase without apocalyptic penalty, but of primary importance will be our ability to produce food in sufficient quantity and of appropriate quality to sustain an acceptable standard of living.”

It is our view that only with the intelligent use of agrochemicals and especially crop protection agents will the food security of future generations be secured. The Farm Ministers of the European Union have agreed to reduce the agrochemicals used in European agriculture, ostensibly to enhance the protection of human health and the environment. This could lead to the exclusion of any pesticide containing active ingredients considered hazardous, with the result that 15% of existing crop protection agents will be deregistered. As for herbicides, this could lead to the loss of active ingredients with an auxin-type mode of action, in addition to pendimethalin, linuron and ioxynil. All valuable components of our crop protection armoury. Ironically, even though these active ingredients could be banned for use by European farmers, we as consumers will still be eating perfectly safe food imported from non- European countries using the very same chemicals! This directive comes at a time when European politicians are, quite rightly, expressing concerns about food security and rising food prices. Yet, this decision could result in much lower crop yields, probably leading to further increases in food costs. It is hoped that the European Parliament will eventually take a more balanced view and that common sense and a pragmatic agricultural solution will prevail.

It is our view that more work is needed to communicate to the general public and EU legislators the distinction between hazard and risk. Thus, the caffeine in our morning coffee or the addition of salt to our food can kill (hazard), but the dose ingested will not (risk). Similar arguments can be presented for the natural but potentially toxic secondary metabolites that feature in our everyday diet, such as in potatoes or nuts. Or, applying the same logic to synthetic chemistry, to shampoos, aspirin and paracetamol. The latter is a most interesting and relevant example of a synthetic molecule that is widely used, since it is well established that paracetamol is hazardous, as it can cause fatal liver damage at high concentrations, but the actual risk of the dose needed to cure a headache is very low.

We hope that this volume will become a useful resource for those working in the plant protection industries and for advanced level undergraduates and postgraduate students of agricultural chemistry, plant physiology and biochemistry, and applied biology.

Andrew H. Cobb

John P.H. Reade

Reference

Copping, L. (2001) The Crop-Protection Industry. *Chemistry and Industry*, Issue 16, 500–501, 20 August 2001.

Chapter 1

An Introduction to Weed Biology

1.1 Introduction

The human race has been farming for over 10,000 years. Weeds would 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)

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 5 families provide 75% of the world’ s food and the same 5 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 (from Radosevich and Holt, 1984).

Number of species classified in 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.) *Alopecurus myosuroides* (L.) *Avena fatua* (L.) *Sorghum halepense* (L.) Pers *Echinochloa crus-galli* (L.)	Couch Black-grass Wild oat Johnson grass Barnyard grass
4	Solanaceae	White potato	*Solanum nigrum* (L.) *Datura stramonium* (L.) *Hyoscyamus niger* (L.)	Black nightshade Jimsonweed Henbane
5	Convolvulaceae	Sweet potato	*Convolvulus arvensis* (L.) *Cuscuta pentagona* (Engelm) *Ipomoea purpurea* (L.) Roth	Field bindweed Field dodder Tall morning glory
5	Euphorbiaceae	Cassava	*Euphorbia maculata* (L.) *Euphorbia helioscopia* (L.) *Mercurialis annua* (L.)	Spotted spurge Sun spurge Annual mercury
6	Leguminosae	Soybean	*Cassia obtusifolia* (L.) *Melilotus alba* (Desc) *Trifolium repens* (L.)	Sicklepod White sweetclover White clover

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.

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 both in terms of 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% 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 $US10 billion, with 50% due to yield reductions and 50% due to the cost of weed control (Rodgers, 1978).

Table 1.2 Problems caused by weeds (from Naylor and Lutman, 2002).

Justification	**Mechanism**
Reduce crop yield	Interference with access to light, water and nutrients
Reduce crop quality	Admixture of contaminating seeds in arable crops Contamination of vegetable crops
Delay harvesting	Conservation of moisture may delay ripening and increase moisture level when harvested
Interfere with harvesting	Climbing plants can make combining more difficult Vigorous, late - growing weeds can interfere with harvesting potatoes and sugar beet
Interfere with	Plants with spines or thorns inhibit animal foraging

animal feeding	
Cause poisoning	Poisoning either through ingestion or contact
Taint animal products	Impart undesirable flavour, e.g. to milk
Act as a plant parasite	Competing for nutrients and water
Reduce crop health	Act as an alternative host for crop pests and diseases Increase vegetation at base of crop increasing moisture and disease
Reduce animal (and human) health	Act as intermediate host or a vehicle for ingestion of pests and parasites
	Photosensitivity
	Teratogens
	Carcinogens
Are a safety hazard	Reduce vision on roadsides
	Risk of fire under electricity lines, on garage forecourts
Reduce wool quality	Hooked seeds reduce value of fleece
Prevent water flow	Plant mass blocking ditches and irrigation channels
Exhibit allelopathy	Release of substances toxic to the growth of crop plants
Impact on crop establishment	Vegetation prevents establishment of young trees Competition for space with establishing crops

Table 1.3 Examples of yield losses due to weeds (from Lacey, 2001, by permission of Oxford University Press; *from Moss, 1987).

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

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

	Estimated loss due 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**

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 (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.

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

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

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 to 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 of this 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 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.

Table 1.6 Some examples of weeds as hosts for crop pests and diseases (after Hill, 1977). Copyright © 1977. Reproduced by permission of Edward Arnold (Publishers) Ltd.

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

In 1994 and 1995 there were several severe outbreaks of the disease brown rot in potato in several European countries, especially in Holland, 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 spreads 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. Copyright © 1977. Reproduced by permission of Edward Arnold (Publishers) Ltd.

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

Table 1.8 The 'successful' weed (adapted from Baker and Stebbins, 1965).

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*