Biology, ecology and spread of weeds of temperate crops

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Summary

Understanding the biology and ecology of weeds is the first step towards fruitful research in weed science. In basic plant ecology the study of stabilized communities has given us a better understanding of the factors governing the composition and development of plant communities. However, in weed science we are faced with labile habitats and pioneer species interacting with agricultural activities. Therefore, the multitude of coming events reduces our ability to predict the future.

The accumulation of knowledge is directed towards management of weeds and modelling future weed infestations and spread.

Introduction

For more than seven millennia human beings have changed the original vegetation by growing crops in monoculture, and during this period weeds have been our faithful companions. In relation to crops, weeds are successful competitors; they reduce crop growth, block waterways and irrigation systems and some are even poisonous to humans and animals.

Weed species are pioneers that increase the diversity of agricultural ecosystems by using the environmental potential, especially developed by human beings for crop production. These pioneer species form the first plant community after a disturbance brought about by harrowing, ploughing, etc. The pioneers pave the way for new colonizing species to gain a foothold, particularly species competitively superior to the pioneers. The presence of weeds on arable land is thus the first step in a succession towards plant communities in equilibrium with the prevailing climate and soil. Consequently, the presence of weed species is just an episode, although an important one, in a succession for more stable plant communities (11,14,20).

One way to study weeds would be to characterize their natural and agricultural habitats. However, some difficulties may appear because some weeds have evolved in parallel with agriculture and therefore are a mere side product of seven millennia of agriculture.

This paper attempts to extract some biological and ecological characteristics of weeds, chosen amongst the infinite, and relate these characteristics to the spread of weeds and the possibilities of predicting future weed infestations.

Biology of weeds

Worldwide, more than 200 species are classified as important weeds. Some of these are cosmopolitans that have invaded farm land from the arctic to the tropics. Others are confined to certain climatic regions (10). The 200 species belong to surprisingly few families of the plant kingdom. Fifty per cent belong to only five families (Table 1).

Table 1 *Important plant families that comprise more than 50% of the world's worst weeds (After 9 and 16).*

Family	Number of species
Poaceae	44
Asteraceae	32
Cyperaceae	12
Polygonaceae	8
Amaranthaceae	7

One of the most cited characteristic of an ideal weed is given by Baker (4). Briefly, it points out that the ideal weed is a plastic annual or perennial that germinates in a wide range of conditions, grows rapidly, flowers early, is self-compatible and produces many seeds which disperse widely.

Most weeds are recruited from labile natural habitats or are aliens introduced by people or other means. Weed surveys in Denmark (56° North) recorded more than 200 species (1,8). Fifty per cent of the most common 80 species naturally occurred on sea shores, sand dunes, lake and river banks, hillsides and forests, whilst the remaining 60% were aliens.

Many aliens have been growing in arable land for so many years that they are naturalized and are considered a part of the 'natural' flora. The weeds in Danish fields are thus no more 'natural' than are the crops. Several valuable crops, e.g., rye and oats, were considered weeds in the ancient days of agriculture. During the long evolutionary history of agriculture, these former weeds have acquired domestic attributes and are today important crops. On the other hand, ancient crop species, e.g., *Spergula arvensis* L., now have gained a foothold as weeds and are interfering with modern crop growing.

Many successful weeds are polyploids and inbreeders that produce stable replicates of readily adapted genotypes. The inbreeding system may be linked with occasional outcrossing permitting adaptation to new or changing ecological conditions. The degree of polyploidy of the natural flora changes with latitude. In Sicily (38° North) about 40% of the flora are polyploids, whilst in Denmark and Spitzbergen (80° North) it is 50 and 80%, respectively (17).

In cereal growing regions of the temperate zones, most weeds are annuals that survive the unfavorable season as seeds in the soil. Figure 1 illustrates that more than 80% of the most common weeds are annuals, and that the displacement between annual and perennial weed species was already in progress well before the introduction of herbicides after World War II (1,8,19). However, it is important to note that some perennial weeds, e.g., *Plantago major* L. and *Cerastium caespitosum* Gil., may act like annuals in annual crop rotation systems.

The soil seed bank is the prime source of recruitment of annual species. Often the size and species composition of the seed bank and the various forms of seed dormancy are important issues that must be addressed to better understand the survival and persistence of weeds in cultivated areas (5).

The viable seeds in the soil often belong to the most common weeds, but correlations between the weed species observed in the field and the sheer number of their seeds in the soil generally are low (12,13). Seed dormancy and germination requirements for many common weed species have been studied in detail and various dynamic models, including soil seed banks, have been suggested (18). Including stochastic processes, which imply the presence of random variables, with Markov-models, where probabilities of transition between life stages are considered, may give more realistic results.

Ecology of weeds

The ecological optimum of a species can be defined in relation to its occurrence in nature. The physiological optimum can be determined under controlled conditions in the laboratory. When we wish to determine the distribution of a species on the basis of eco-physiological characteristics, we cannot uncritically use the alleged ecological nor the physiological optimum, because the distribution and growth of a species are confounded with the competitive ability of its fellow species in the plant community (19,22,23), the climate and the soil (1,2,3). Consequently, basic studies of eco-physiology of weeds in arable land must be followed by studies of the species under natural environmental conditions.

One major concern in weed ecology is to unravel the effects of crop husbandry, soil and climate upon the weeds.

In a recent study the distribution of weed species in response to eight crops and seven edaphic factors was evaluated using multiple linear logistic regression with adjustment for over-dispersion. Crop type and sampling year were used as classification variables. The regressions showed that crop type is an important factor governing the distribution of 37 common weeds in the eight crops (2) (Figure 2). Some detailed studies showed that *Viola arvensis* was favoured by decreasing potassium and clay content. Crop type and potassium affected the occurrence of *Stellaria media*. The occurrence of *Poa annua* was influenced by crop type and organic matter, with a significant interaction (3).

The phytosociological association of crops in relation to the weed flora has been studied on several occasions (19,21). Factor analysis can graphically give a general idea of how crops affect the weed flora (Figure 3). The placement of crops in Figure 3 is extracted from the intercorrelations of crops based upon the frequencies of weed species in the respective crops. The winter annual crops in Figure 3 had high loadings on factor 2, whilst the summer annual crops had high loadings on factor 1. In a phytosociological context, the factor analysis is showing a continuum based on the 'summer annual factor 1' towards the 'winter annual factor 2'. The composition of the weed flora is a product of the growth period and competitive ability of the respective crops. The diversity of the weed flora differed between crops as also indicated in Figure 2, but the weed flora of crop types with the same life duration showed similarities.

In most crops of the temperate regions, the diversity of the weed flora is rather restricted. In Danish studies 80% of the flora was represented by only 20 out of about 200 recorded species (Figure 4).

Depending on the intensiveness of agriculture, the growth of crops, previously confined to certain soil types, is nowadays often determined by the intensity of fertilization. Consequently, the effect of crops upon the distribution of weeds need not exclusively be a matter of the crop and soil types per se, but could also reflect the history of these crops, such as seed bed preparation, soil cultivation etc.

The same trends as seen in Figure 3 also apply when looking at the same crop type growing in regions of contrasting climate; factor analyses of Australian data showed that regions of low rainfall were distinctly separated from regions with high rainfall (21).

On the basis of the evidence above, it is not surprising that exceptions from the rule of the ideal characteristics of weeds, given by Baker (4), are common.

Spread of weeds

The spread of weeds is easiest to study for alien species. Therefore, the epidemiology of weeds has been most rewarding in North America and Australia. Newsome and Noble (15) concluded from an Australian study that successful aliens have some common eco-physiological characteristics that perhaps explain their invading ability in temperate regions. The species tend to be specialists with restricted requirements for germination, growth, etc., rather than generalists. But the eco-physiology of plants is too complicated to fit into schematic categories of invaders and non-invaders.

On the basis of herbaria material, Forcella (6,7) investigated rate of initial spread, final distribution and pattern of migration of alien species in Northwestern USA. Particular models predicted the initial rate of spread and the potential areas occupied. Aliens with high initial rate of spread are likely to become a nuisance (Figure 5). Weeds with low rates of spread may remain unimportant in larger areas; but they can, of course, pose serious problems in restricted areas.

Aliens with high rates of spread or wide distribution in their native regions should be controlled, and in countries with traditions for proclaiming legally noxious weeds, this should be done when their distribution is still limited. To the best of the authors' knowledge, no proclaimed weeds have yet been eradicated after introduction.

Although most areas of fertile soils in the temperate regions have been in cultivation for many years, the migration pattern of alien weeds may help us to point out future weed problems from 'new' species.

Concluding remarks

The biology, ecology and epidemiology of weeds raise an infinite number of important questions. Only very few of these have been addressed in this paper. Weeds tempt providence on agricultural land and have proved their survival skills in spite of the hinderance humans impose upon them. We are well aware that crop production pattern, soil, climate and migration of weeds are important factors in understanding the weed-crop ecosystem; but when it comes to forecasting events, we often are in the same position as insurance sellers. They know the probability of making a profit, but they cannot forecast what is going to happen to individuals.

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Figure 1 Proportion of common annual and perennial weed species in Danish Spring cereal recorded in three surveys. The shift towards annuals commenced before the introduction of modern herbicides after 1945. (From 8).

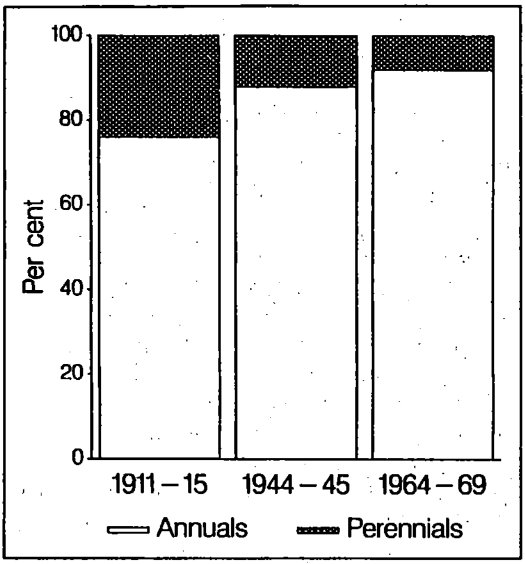

Figure 2 Number of 37 species significantly affected by various ecological factors. [OM = organic matter]. The significance of factors was adjusted for the effects of all other factors in the analysis (From 2).

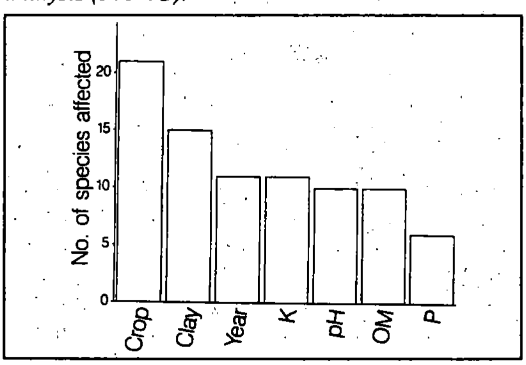

Figure 3 Factor pattern of crops (O summer annual crops; # winter annual crops) based on weed frequencies (Adapted from 1).

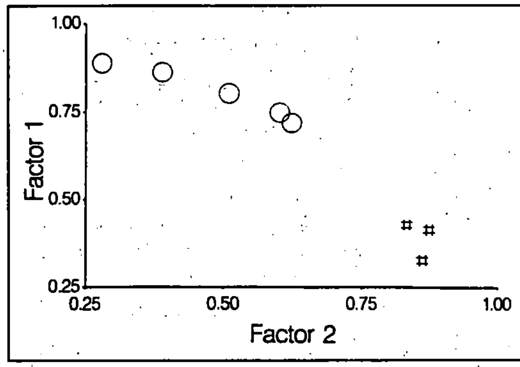

Figure 4 Percentage of accumulated frequencies of recorded weed species in spring barley, sorted after decreasing frequencies. (Adapted from 1).

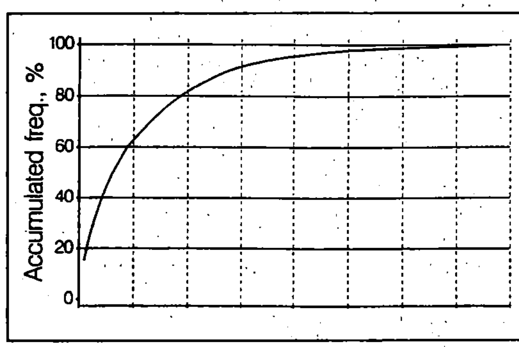

Figure 5 Schematic spread of alien weeds in response to time after introduction. A species covering the whole available area and two other species with only limited capacity for spread.