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WEED SPECIES AND WEED COMMUNITIES*

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Bowing to the mower,
Yet they know nothing about classification.
Happy little weeds.

Hō-Ru Tsu-na

Introduction

One of the most satisfying experiences of phytosociological work is the moment when out of the mass of amorphous data begins to crystallize a lattice of general principles and an understanding of vegetation and its ecology. But if one works still further and gathers more and more knowledge in one and the same field, one reaches a deeper level. The more one knows, the more the boundaries of classes are broken down, the crystals loose their defined shape again and one begins to understand the impossibility of classifying nature in a generally satisfying way. If one tries to retreat to the classes of individuals called species, one has soon to admit that, here too, with growing knowledge the boundaries become insecure, especially where the notoriously heterogeneous weed species are concerned. Here one approaches the boundary between science and philosophy. As this is to be a scientific paper we have to stop here and try to maintain classification as a mere practical means to get a general view and to summarize and pass on our knowledge to others.

Weeds are a class of plants that is difficult to define (if one knows too much about them) as it has no sharp boundaries. A vast literature deals with this problem (summarized in Harlan & de Wet 1965, King 1966). For our purpose we shall define weeds as plants adapted to man-made habitats and interfering there with human activities. Weed species are, therefore, plant species that meet this definition in at least a part of their area. Many, but not all weeds are typical colonizing species, but not vice versa as often maintained, as there are many colonizing plant species that cannot be considered as weeds.

Weeds may occur in three general types of vegetation: (1) As agrestals (or segetals) in arable land; (2) As ruderals in one of the large range of possible ruderal sites; (3) In natural vegetation, from which they originate or into which they have been able to invade.

The results presented here are the general conclusions from the data of extensive phytosociological field research into weed vegetation on arable land and ruderal sites all over Austria (about 2.000 relevés), in Southern Europe and (together with Prof. Dr. E. Hübl) Southwest Iran. The phytosociological results have previously been published in part only (Holzner 1970–1974b, Hübl & Holzner 1974) but some of the general aspects have already been published briefly elsewhere (Holzner 1974a, 1977).

Ecological and sociological behaviour of two opposite types of agrestals in the different parts of their geographical range

Type A: It is generally accepted that many of the European agrestals, especially those of autumn-sown cereals, were brought from the Middle East, the "cradle of agriculture", and the Mediterranean to Central Europe. From there they were spread over the whole world. It is a group of annuals adjusted to a climate with an adverse season, which they endure as seeds. They occur in different types of natural and semi-natural communities from the Orient to Southern

* Nomenclature follows Ehrendorfer (1973), Phytosociological units according to Westhoff & Den Held (1969).
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Europe, some of them even in Central Europe, in places where conditions for perennials are so severe that they do not form dense stands, leaving enough space among them for shortlived pioneers. Their range has been enlarged by man as agriculturist, who created open habitats, distributed their seeds and brought them to each country in Europe. In many places they can only survive by the involuntary help of man, creating for them sites free from the competition of most species of the native flora. In these countries we can observe a great difference between the flora of cultivated land and the flora of the natural and seminatural vegetation, which is not the case in the Mediterranean and particularly the Middle East where many of the weeds occur in cultivated land and in the adjacent more or less natural vegetation (Kühn 1972, Zohary 1973). This seems to be an important argument, but we must not overlook the fact that these areas have been under intensive human influence for thousands of years and that overgrazing in particular opened the natural vegetation to colonizing annuals. Thus, an answer to the question of the origin of many weed species will always be a rather doubtful one and it is very likely that many weed species have evolved rather recently under cultivation pressure ("homeless weeds": Zohary, M. 1973). (As it is not the purpose of this paper to discuss the origin of weeds I can only refer to the literature (e.g. Baker 1965, 1974, Zohary 1973).)

From a Central European point of view the weeds of type A are thermophilous species of southern origin, occurring as weeds mainly in winter crops, where they are adapted to the germination conditions and to the seasonal rhythm of the cereal species that have come from the same area. In the classical Phytosociological System (cf. R. Tüxen 1950, Westhoff & den Held 1969), the species of type A are in general identical with those characteristic for the*Secalietalia*. If we consider the whole range of this order we can observe a gradual impoverishment mainly related to the declining summer temperatures, from the south (and east) to the north (and west) as one species after the other drops out but very few are added, acting, in a way, as indicators of cool and humid climates. The same phenomenon can be observed with increasing altitudes in the alps. In a somewhat exaggerated sense we could say with Kühn (1972) that the European weed communities of winter crops on basic soils are just depauperate forms of the oriental ones.

As the complex climatic gradient that is relevant to this group of weeds usually shows a smooth transition, the alteration of the species-composition in weed communities is a very gradual one leading to a "continuum" between the rich, southern and the poor, northern communities. Thus it is difficult to classify distinct community types within this transition zone, if one is considering a large area.

Before the species reach the northern (western, upper) limit of their range they show a typical preference for calcareous soil, while in their optimal climatic region they are indifferent to this soil factor. Thus in Eastern Austria for instance the same *Caucalidion* communities can be found on acid as well as on calcareous substrates, because the floristic dissimilarities between the weed communities on the different substrates are much smaller than between the communities in cereals or row-crops (see below).

Thus, the general ecological description of the *Caucalidion* as an alliance of weed communities on calcareous substrates as is generally accepted in the literature (Tüxen, R. 1950) is valid only for areas near to its climatic boundary.

I have the impression that at least for weeds the number of "calciphilous" species is much smaller than usually accepted (if there are any at all), as most of the many weeds that are labelled as calci- or basiphilous in the European literature grow well on acid soils if the climate is optimal for them.

One of the effects on weeds of intensified agriculture is that many sensitive species diminish their range of distribution by retreating towards its centre because they are more sensitive and less vigorous at the limit of their range. *Secalietalia*, especially *Caucalidion* species, have become extinct in many parts of Northern, Western and Central Europe because climatic conditions there are not optimal for them.

Type B represents a similar gradient to A not from warm to cool but from oceanic to continental climate* as is shown by species of the *Aperetalia* and lower syntaxa belonging to this order, species which have an oceanic-suboceanic distribution centre and are acidophytes, a combination often found in European plants. Their origin is even more mysterious than that of the former group. It is probably not the Middle East (Kühn 1972) but Southwestern Europe, where they have their natural habitats in open communities on poor sand or shallow granitic soil. With human help they were able to invade as weeds the continental areas of the rest of Europe. Today they are retreating again because they cannot withstand the double stress of unfavourable climate and intensified agriculture. They are especially sensitive to intensified fertilization

* To maintain the theme and general approach of this paper, geographical matters and chorological peculiarities of the species are simplified in a rather crude manner. For details see Meusel, Jäger & Weinert (1965) and Weinert (1973).

because it enhances the strength of other weeds that were not able to compete with them on the poor soils.

While calciphily often seems to be a function of climate rather than a physiological feature of the plants, many acidophytic species really need acid soils, or better expressed, have to avoid calcareous ones because of their special physiological properties (cf. Kinzel 1968, 1969, 1971). If the climate is optimal and competition is low some of them are able to compete on rich, even neutral soils. But in continental and subcontinental areas they are able to compete only in very acid and poor soils.

These results of ecological field-surveys show us that the reaction of plant distribution to the complex of soil properties, indicated by the pH values, is a complicated one and a function of (complex) climatic factors and the competition of other species, and it can therefore vary from one site or part of the species area to another.

If one attempts to derive general principles from findings on such a special group of plants as annual weeds, it could be said that the number of calciphilous species will turn out to be much smaller and that of genuinely calcifuge species (for physiological reasons) larger than usually accepted, if the whole area of the species and the complex dependence on climate and competition are taken into account. Though alpine vegetation has always been the primary and the most impressive area for demonstrating the floristic differences between carbonaceous and siliceous substrates, the same results can be expected there, as has been shown recently for instance by our own observations (Holzner & Hübl 1977) in eastern Austria and more particularly by the experiments of Gigon (1971) in the Swiss alps.

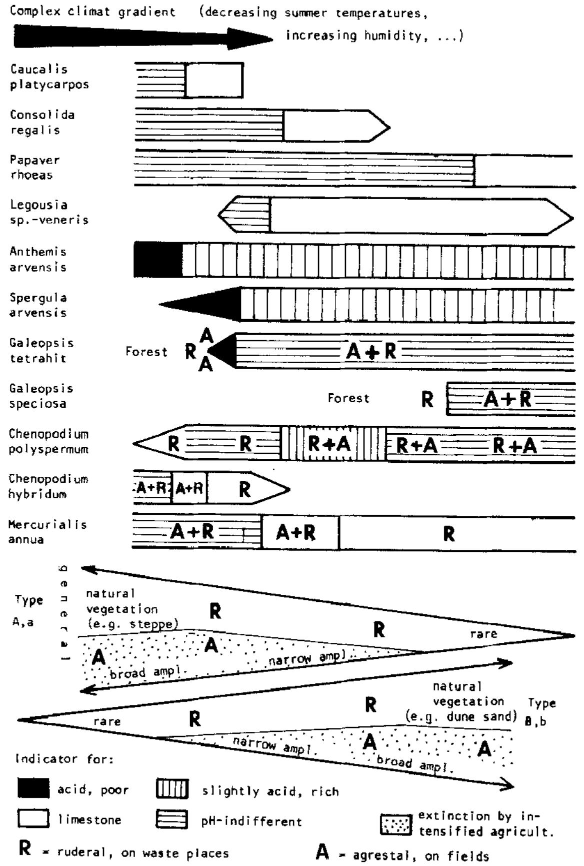

Fig. 1. Variability of ecological and sociological behaviour of some weed species in Austria with the climate.

Distribution of weed species in ruderal and agrestal vegetation types respectively depending on climatic factors

While the discussion has so far been mainly about agrestal species, weeds that may occur on ruderal sites as well as on cultivated land will now be dealt with. Many of them are typical pioneer species (characteristics cf. Baker 1965, Ehrendorfer 1965, Harper 1965). In arable land they occur primarily in so-called "row-crops" (maize, turnips, potatoes), crops that are sown late in spring and harvested in autumn, and, at least in former times, were hoed several times. The row-crop weeds are characterized mainly by high temperature requirements for germination (Lauer 1953), some of them also by short life cycles and high nutrient requirements. In the phytosociological system the row-crop weed communities are united in the *Polygono-Chenopodietalia*.

Type a: Termophilous species requiring high summer temperatures, mainly species of *Eragrostidion* but also *Panico-Setarion*, occur in their optimal climatic areas in ruderal as well as agrestal vegetation. The cooler the climate, the more they are restricted to ruderal sites only. For this phenomenon there could be three reasons: Many ruderal sites have a microclimate warmer than the general climate of the area (Grosse-Brauckmann 1953), and many ruderal sites are richter in nutrients and often contain more lime (from walls, etc.) than the agrestal sites nearby. The most important reason in my opinion is that in young or often disturbed ruderal sites which offer the suitable environment for the colonizing plant species in question, there is much less competition than on cultivated land, where the weeds are not only subjected to the competition from other weeds but also from the cultivated plants, which are sown as densely as possible.

If we observe the sociological and ecological behaviour of species in this group, we see a combined effect of increasing restriction to communities with little competition from other species on ruderal sites and increasing preference for calcareous soils with decreasing summer temperatures (see Fig. 1).

Type b: Among the ruderal/agrestal species we are talking about, there is also a group with its distribution center in subatlantic (or even atlantic) areas. While they occur in their optimal climatic regions as agrestals and ruderals as well, in a subcontinental climate they are not able to compete on other than ruderal sites and in a more continental climate they finally retreat into very shady sites, gardens or even forests. J. Tüxen (1958) has reported on the differences in weed species combinations in gardens and row-crops of the same area.)

Influence of modern agriculture on the distribution of weeds

During the last few decades a kind of revolution in agricultural methods has taken place. Most tools and techniques that have been in use for centuries more or less unaltered have been abandoned or replaced. With increasing standards of living, high wages and shortage of workers, farmwork had to become rationalized and mechanized. As human actions are the most important ecological factors for weeds, their distribution and communities have been subject to strong alterations, a development that is still going on.

One of them has been the extinction of many species in Central Europe (R. Tüxen 1962, Westhoff & Zonderwijk 1960, Zonderwijk 1975, Kump 1970) that have accompanied the cropplants there for centuries. As I have pointed out in a previous section these plants are only locally eradicated and are retreating towards their climatic optimum, where most of them will be able to survive somewhere in the vegetation outside the fields or perhaps even within them.*

Characteristically those species vanish first that were already rare in the area followed later by those that have been indicators of extreme conditions (especially of the soil). There is a whole complex of agricultural measures that caused these alterations. Their effect can be summarized in general with "levelling of ecological conditions". What the farmer simply does is to try to get the conditions in the field as near as possible to the physiological optimum of his crops which means for most factors trying to get away from extremes: acid soils are supplied with lime, wet ones drained, dry ones irrigated and fields in areas that cannot be meliorated by artificial means are abandoned or used for other purposes. This levelling means that weeds with requirements near to those of the crop species will thrive, while those disappear that are adapted to worse conditions but cannot compete. Thus the argument often cited that weed communities are no indicators any more, is clearly wrong; uniform weed communities indicate the uniformity of environmental condititions. The indicators of optimal conditions not only supress the other weeds, they are also strong competitors with the cultivated plants. Thus a necessity for intensified weed control arises.

Usually the drastic alterations in the composition of weed communities have been attributed to the use of herbicides. As I have already pointed out there is a complex of other factors that is one of the main causes for this development. The use of herbicides is not the only one but the most drastic factor. (For a more detailed survey of the influence of modern methods on weed distribution see Bachthaler 1968).

Influence of herbicides

Sensitive species are driven back to areas where they can find refugial sites, as described above. In many countries they are completely eradicated. The outcome is the decrease of competition of other weeds with the resistant species. Thus the use of herbicides has afforded competition experiments on a huge scale. How do species in a plant community behave if most of their competitors are removed?

Resistant species have now become able to grow in greatly increased densities and with single individuals much larger than before (as is described e.g. for the Netherlands by Zonderwijk 1975, for Austria by Neururer 1966, Szith 1977). This development is called compensation (Rola 1973), resulting in weed communities poor in species, but with high densities of individuals. The second phenomenon is that resistant species are also able to enlarge their range of distribution and to fill the niches of the eliminated species, conquering new areas where they were not able to compete before. This development is a further proof of the theory, especially elaborated by Ellenberg (1950, 1963, 1968), that the ecological behaviour of species is dependent on the competition of others and vice versa,

* There are some extremely specialised species (crop-mimics) that are actually threatened by extinction in their whole area; weeds that have lost most of their colonizing abilities and are dependent on being sown with the crops.

the competitive power of a species depending on the environmental conditions.

From an ecological point of view the enlargement of areas of the resistant weeds takes place in two general directions:

(1) Towards ecologically adverse conditions

(1, 1) climatically adverse, e.g. migrating to the north, *Sorghum halepense*, *Avena fatua*, ...

(1, 2) Adverse soil conditions e.g. *Avena fatua* occurring on poor soils, where it never occurred before (Prante 1970, Holzner 1973), or ruderals becoming agrestals (*Datura*, *Descurainia*, *Galium aparine*, ...)

(2) Towards their physiological optimum: Poorly competing species that have been only able to survive at the limit of their physiological tolerance are able to invade better sites, because of the lack of competitors (e.g. *Digitaria ischaemum*).

The following scheme is used to illustrate the general development of weed vegetation after several years of regular usage of herbicides.

General example for a compensation series:

Weed species A, B, C, D, E, F, G, H, I, J, K, L, M, N, O, P.
A ... dominant, a ... sparse
R = ruderal weeds
F = agrestal weeds from adjacent region
E = introduced exotic species

Herbicides 1, 2, 3, 4, ...

A, B, C, d, g, h, i, j, k, l, m, n, O, P $\xrightarrow{1}$ B, c, g, h, k, m

$\xrightarrow{2}$ G $\xrightarrow{3}$ C, R, F, E $\xrightarrow{4}$ ....

The evolution of weed species is still in progress and is furthered unintentionally by man as he is bringing together species and races that have been separated geographically or ecologically, giving them the opportunity for hybridization, introgression and polyploidization, and by increasing the mutation rates of weeds by the use of herbicides (Mohandas & Grant 1972, Harper 1956, Grant 1970). The current speed of weed evolution is best demonstrated by the increasing genesis of resistant ecotypes (Szith 1977) ("herbicidotypes") in hitherto sensitive species. There will be a continued shifting of weed distributions, resistant weeds invading communities where they did not occur before and the formation of quite different, new weed communities.

Problems of classification

Classification of weed communities into abstract community types according to the rules of the Zürich-Montpellier school (Braun-Blanquet 1964, Westhoff & van der Maarel 1973, Werger 1974) has always been difficult, as is proved by the many alterations that have been made in this part of the system and the new concepts specially developed to press the "obstinate" weed communities into the system (e.g. Brun-Hool 1966, Kopecky & Hejny 1974). The main reasons for these difficulties are:

(1) Weeds are not only dependent on the so-called "natural" environmental factors but also strongly on the complex of anthropogenic factors that are difficult to comprehend. "Chance" plays a big role influencing the occurrence of weed species in communities.

(2) Agrestal weeds, most of them being often short-lived annuals, react quickly to alterations of the environment. Thus, the composition of weed communities can vary strongly from year to year, depending on the weather and human measures, but also from season to season of one year, forming distinct spring, summer and autumn aspects.

(3) Weeds often are "ubiquitous" species with a large amplitude often caused by phenotypic plasticity and heterogeneity within the species, which is typical for colonizing species.

(4) The phytosociological system for weed communities was propounded in Central Europe, an area where many agrestal weed species occur at the very edge of their distribution. The rich weed vegetation of Southern Europe and the Middle East is practically unknown to science.

(5) The alterations in agrestal weed communities described above have made weed sociology even more difficult.

(6) Many agressively colonizing ruderals tend to form dense stands dominating large areas by the combined means of vigorous vegetative reproduction and allelopathic influence (Numata 1974, 1975, Rice 1974). These communities dominated by one species are difficult to integrate into the floristic system.

A typical example of the problems which weed communities offer in classification is the scientific controversy about the integration into the system of three different weed communities which may be developed within one year on one and the same field.

Especially in warmer areas of Europe, e.g. in Eastern Austria, in spring a rich community (1) may be observed of short-lived winter annuals (e.g. many *Veronica* spp.) that germinate mainly in autum, ripen their seeds in late spring and very soon perish. If relevés are made in June no "traces" of them are left whereas in the table the spring relevés show a clear, distinctive block of species. This community is followed (2) by one of weeds that also germinate in autumn or in spring but ripen their seeds with the grain crops. Groups (1) and (2) are best developed in autumn-sown cereals. Group (3) consists of summer annuals requiring a high soil temperature for germination (Lauer 1953). They germinate and ripen with the row crops but can also be found in the stubble of the cereals.

Different authors have had different concepts to describe these communities and to fit them into the system. Today two extreme versions have become established: (A) The three communities are to be regarded as aspects of one association and (B) the first community is ignored and (2) and (3) are separated at the highest level of the system, they are regarded as different classes (*Secalietea* and *Chenopodietea*). Both views have good arguments to offer and a lot of paper was used to discuss them. But the question whether (A) or (B) is true has no meaning at all as it is only a question of conventions. It is therefore useless to discuss the arguments presented by the supporters of these diametrically opposite points of view. (A discussion of the extensive literature on this topic has already been given by Hilbig (1967), Schubert & Mahn (1968), Kropác, Hadac & Hejný (1971).

The purpose of this example was to illustrate one of the severe problems of contemporary phytosociological weed community systematics. The original aim of the system was to give a practical and reasonable order and comprehension and this is even more obstructed by the proliferation of associations that are described from a very local point of view and are very similar in species combination (especially within the *Panico-Chenopodietalia*). Even worse is the habit of making alterations in the higher ranks of syntaxa without a complete review of the whole range of distribution of the syntaxon concerned.

Thus, if we are to have a useful system of weed communities we shall need more flexibility avoiding too rigid rules, and the inclusion of ecological knowledge as it is e.g. also proposed by Kojić (1976).

Conclusions

The area a weed species can occupy depends on ecological factors (including anthropogenic ones) and competition of other species. As most of them are colonizing species, it can be assumed that they are able to invade each suitable habitat within the distance they can reach with their diaspores in a rather short time. Transport by man over vast distances plays an important role by forming new centres of dissemination. The main factor determining areas of distribution is a climatic one (first level factor, Numata 1962, 1967). In their optimal climatic area, which is often also their presumable native one, weeds show the strongest competitive power and the widest ecological and sociological amplitude and are able to occur within a wide range of different soil conditions and within many types of plant communities.

It is well known (Ellenberg 1950, 1963, 1968, Werger & van Gils 1976) that many plant species have a narrower ecological amplitude towards the edge of their range than in the center. Weeds are plants spread by man far beyond their original range, thus occupying a large "border area" (e.g. for many weeds the whole of Central and Northern Europe), where climatic conditions are suboptimal to them and where they can only persist with the help of man as agriculturist. Here they are rather weak competitors and have a narrow ecological and sociological amplitude. Some occur on soils with extreme conditions because they are especially sensitive to the competition of other species and cannot compete in better stands, others are restricted to the habitats nearest to their physiological optimum or offering conditions able to replace the most important missing factor at least partly (Walter & Walter 1953).

In this geographical (and ecological) border area many agrestals are especially sensitive to the measure of rationalized agriculture (in general the ecological levelling of soil conditions and the use of herbicides), and retreat towards their optimal (and original) areas, becoming extinct in many parts of Central Europe. The behaviour of resistant species after the extinction of many of their competitors by herbicides proves Ellenberg's theory, that the distribution of plant species is dependent on environmental factors and the competition of other species. The competition of other species weakens the power to withstand adverse environmental conditions and vice versa adverse environmental conditions weaken the competitive power of species.

Thus, the observation of weed species and weed vegetation provides us with good insight into the mutual action of competition and environmental factors and its results, the distribution, ecological and sociological behaviour of plant species.

Summary

With weeds as with many plant species the main or first level factor determining the area of distribution is a (complex) climatic one. As they have an artificially enlarged area of distribution, they have a huge border area (in an ecological sense), where the climate is not optimal for them, and where they have a narrow ecological and sociological amplitude and are especially sensitive to some measures of modern intensified agriculture. In their northern border areas species of southern origin are restricted to calcareous substrates and to agrestal and finally ruderal communities, while in their optimal climate they are indifferent to that soil factor and able to compete with other species even in natural vegetation types. Species presumably of origin in atlantic areas are restricted with increasing continentality to very poor and acid soils, as they cannot compete with other species on better sites any more, because of their physiological properties. Thus weed distribution demonstrates the complicated reaction of plant species to the complexes of soil-climatic factors and to the competition of other species. As far as weeds are concerned, species may be only relatively calciphilous, but genuinely calcifuge species, the control being climatic in the former case and physiological in the second.

The measures of modern agriculture bring about a gradual extinction of sensitive species from the limit of their range towards their centre of distribution, where they can find refuge habitats in the natural vegetation. The sensitivity of such species (also against herbicides) seems to increase towards their limits. Resistant species occur with increasing densities after the removal of their competitors. In addition, they are able to enlarge their area and to invade sites, where they had not been able to compete before, or sites where they could not previously bear the environmental conditions together with the competition of the rich weed flora.

As the complex climatic gradients responsible for the ranges of weed species show smooth transitions, the alteration of species composition in weed communities is also a gradual one. This is one of the problems of weed phytosociology briefly discussed.

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