Preslia, Praha, 64:45-51, 1992

Population characteristics of expansive perennial herbs

Populační charakteristiky expanzívních vytrvalých bylin

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Prach K. et Wade P. M. (1992): Population characteristics of expansive perennial herbs. - Preslia, Praha, 64:45-51.

K e y w o r d s : Expansion, perennials, population characteristics, quantitative measures

Some perennial herbs which have expanded in recent times in the temperate zone of Europe were evaluated using criteria for an 'ideal weed' adapted from Baker (1965). Data were gathered on relative growth rate; production dispersibility and viability of diaspores; intensity of vegetative spread; timing of the first generative reproduction; and maximum height of species. The range of conditions suitable for germination, and self-compatibility were also considered. On the basis of these data, semiquantitative and qualitative criteria were used for a comparison of the species based on an estimation of their expansive ability. A high expansive ability was found in all of the following species listed in decreasing order: *Urtica dioica; Cirsium arvense; Typha angustifolia/latifolia, Chamerion angustifolium, Artemisia vulgaris, Baldingera arundinacea; Calamagrostis epigeios; Tanacetum vulgare; Agropyron repens*, and *Tussilago farfara*. The best strategy, facilitating a species expansion is the high production of easily dispersed diaspores (in space and/or time), in combination with efficient vegetative propagation, unless the establishment of species is limited only to very specific habitats.

Introduction

Baker (1965) defined an 'ideal weed' on the basis of population characteristics: An 'ideal weed' should be a plastic perennial which germinates under a wide range of environmental conditions, grows quickly, flowers early in its life-span, is self-compatible, produces many seeds which are easily dispersed, reproduces vegetatively, and is a good competitor. The criteria were later accepted in some papers dealing with invasive plants (Drake et al. 1989) and also enlarged on by Roy (1990). It is not, however, necessary for a weed or an invader to exhibit all these characteristics (Noble 1989).

The criteria may also be accepted as an approximate evaluation of the expansive ability of plants as defined below. Expansion is often a result of increasing frequency of various perturbations throughout the area. Expansive species are capable of colonizing perturbed sites. Life history characteristics of colonizing plants surveyed by Bazzaz (1986) overlap with Baker's view. Some population characteristics of colonizing plants were also discussed by Grime (1986).

Most of Baker's criteria can be quantified but relevant quantitative data, however, are scattered in many papers. Data were gathered on some perennials commonly occurring in the temperate zone of Europe and expanding at least in some regions, mostly in central Europe. The present paper is based on both literary and original data (partly published in Prach 1988).

The use of terms expansion, invasion, and colonization as used in this paper are defined as follows:

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I n v a s i o n - rapid increase in occurrence of an alien species in a region.
E x p a n s i o n - (a) rapid increase in dominance of a species in a particular locality; (b) rapid increase in occurrence of a native species in a region as evaluated in this paper.
C o l o n i z a t i o n - establishment of species in newly created habitats.

Methods

For the purpose of the present study, the criteria used by Baker (1965) were slightly adapted and most of them were specified more precisely. Each species was assessed by field observations in Czechoslovakia and through data presented in the European literature or exceptionally from North America. The species were selected *a priori* through field experience, being considered as some of the most expansive. Two non-expansive species were evaluated for comparison. Phenotypic plasticity emphasized by Baker was omitted because of its difficulty to quantify. Thus, the following characteristics were considered and classified into qualitative or semiquantitative categories (for detailed methods used in assessing the characteristics see the respective references):

(a) Perennial: yes +; no 0

(b) Germination under a wide range of environmental conditions without complicated dormancy mechanisms: yes +; no -

(c) Maximum relative growth rate of seedlings (after Grime et Hunt 1975, Grime, Hodgson et Hunt 1988): RGR_{max} ($g.g^{-1}.week^{-1}$) higher than 2.0 +++; from 1.0 to 2.0 ++; from 0.5 to 1.0 +; less than 0.5 0

(d) Early generative reproduction, i.e. time of the first fruiting: usually within one season +++; usually in the second year ++; usually in the third year +; later 0

(e) Self-compatibility (listed in Frank et Klotz 1990): yes +; no 0

(f) Maximum production of diaspores: more than $100,000.m^{-2}.year^{-1}$ +++; 10,000-100,000 ++, 1,000-10,000 +; less 0

(g) Dispersibility of diaspores:

In space: light anemochores with pappus +++; heavy anemochores, light anemochores without pappus, hydrochores, and zoochores with occasionally very long dispersal distance ++; others with usual dispersibility up to c. 10 m +; barochores with dispersal around parent plants 0

In time: longevity of diaspores often more than 10 years +++; usually 3-10 years ++; usually 2 years +; usually one season and less 0

(h) Vegetative spread: intensive vegetative spread by rhizomes and stolons to a distance often more than 0.5 m a year +++; vegetative spread by rhizomes and stolons to a distance usually less than 0.5 m a year ++; intensive lateral growth without rhizomes, stolons, etc. +; no vegetative spread 0

(i) Competitive ability is expressed in the simplest way (see Grime 1979, Keddy 1989) by usual maximum height of plants, including inflorescences or fruiting body: plants often higher than 1 m +++; usually 0.5-1 m ++; usually 0.2-0.5 m +; less than 0.2 m 0

Results

Using the given criteria, 6 broad-leaved herbs and 4 graminoids were evaluated. Two more plants occurring in anthropogenous habitats were added for comparison:

Table 1. - Evaluation of the potential expansive ability of the species.

Species: / Characteristic:	*Agropyron repens*	*Artemisia vulgaris*	*Baldingera arundinacea*	*Calamagrostis epigeios*	*Chamerion angustifolium*	*Cirsium arvense*	*Tanacetum vulgare*	*Tussilago farfara*	*Typha angustifolia and latifolia*	*Urtica dioica*	*Anthoxanthum odoratum*	*Prunella vulgaris*
Perennial	+	+	+	+	+	+	+	+	+	+	+	+
Germination under wide range of environmental conditions	+ [8]	+ [11]	+ [11]	+ [1]	+ [11]	+ [7]	+	+ [11]	0 [9]	+ [4]	+ [11]	+ [11]
Seedlings RGR	++ [11]	(++)	++ [6][11]	(++)	++ [11]	(++)	(++)	++ [11]	(++)	+++ [6][13]	+ [11]	+ [11]
Early generative reproduction	++ [8]	++ [11]	++ [12][5]	+++ [1]	++ [11]	++	++	++ [11][13]	++ [9]	+++ [5]	++	++
Self-compatibility	0 [8]	+ [16]	0 [11]	0 [16]	+ [11]	0 [7]	+ [16]	+ [11]	0 [9]	0 [4]	0 [11]	0 [11]
Production of diaspores	+ [2][8]	+++ [2]	++ [11]	+++ [2]	+++ [2]	++ [7][2]	+++ [2]	++ [2]	+++ [9]	+++ [4]	+	0
Dispersibility of diaspores:												
in space:	+	++	++	+++ [2]	+++ [2]	+++ [2][7]	++	+++ [2]	+++	++	+	(++)
in time:	++ [8]	++ [3]	+++ [3]	0 [1]	0 [3][14]	+++ [3][7]	0	0 [3][11]	++ [3]	+++ [4]	++ [11]	0 [15]
Vegetative spreading	+++ [8]	++ [11]	+++	+++ [1]	+++	+++ [7][11]	+	+++ [11]	+++ [9][10]	+++ [4]	+	++
Maximum height	++	+++	+++	+++	+++	+++	+++	0	+++	+++	+	0
Sum	15	19	19	18	19	20	16	15	19	22	11	9

1) Dolečková et Osbornová (1990); 2) Prach (1988); 3) see Milberg (1990) for original references; 4) Basset at al. (1977); 5) Šrůtek in Prach (1989), **Šrůtek pers. com**; 6) Grime et Hunt (1975); 7) Moore (1975); 8) Werner et Rioux (1977); 9) Grace et Harrison (1986); 10) Fiala (1978); 11) Grime et al. (1988); 12) **Klimešová, pers.** com.; 13) Ogden (1974); 14) Thompson et Grime (1979); 15) Winn (1985); 16) Frank et Klotz (1988).
Other data: unpublished author's observations and trivial statements.
( ) Estimations without exact data.

Anthoxanthum odoratum, representing a non-expansive grass, and *Prunella vulgaris*, a non-expansive herb. Results are summarized in Table 1. If the pluses are summed, the following order of species according to decreasing ability to expand is obtained: *Urtica dioica; Cirsium arvense; Typha angustifolia/latifolia, Chamerion angustifolium, Artemisia vulgaris, Baldingera arundinacea; Calamagrostis epigeios; Tanacetum vulgare; Agropyron repens,* and *Tussilago farfara.*

Discussion

All of the species considered to be expansive attained a high 'score' in the evaluation. This implies, among others, that there is a close correlation between the empirical field knowledge on behaviour of the species and their real population characteristics.

The procedure suggested here could be applied to other species including newly introduced species (potential invaders) to help prediction of their invasive potential. The next step following the evaluation should be to combine it with a quantification of the ecological amplitude of a species, and of availability of suitable habitats in a landscape. This would enable more precise prediction of expansion of species. We believe this way is promising for future research to project population ecology into a landscape scale. Unfortunately, similar attempts have been stressed only rarely (Grime 1986, Grime, Hodgson et Hunt 1988).

All species evaluated in the paper are native in the considered geographical region. They exhibit at least some features typical of competitive ruderals (C-R strategists) sensu Grime (1979), though Grime himself does not include all of them as C-R strategists (e.g. *Chamerion angustifolium, Urtica dioica, Baldingera arundinacea*).

Three basic groups of ruderal species were characterized in Prach (1989): (a) Species adapted to habitats mechanically disturbed by a single, intensively disruptive event. (b) Species adapted to habitats affected by chronic mechanical disturbance of lower intensity (e.g. trampling), or permanently stressed (e.g. input of toxic agents). (c) Species expanding in habitats exposed to increasing nutrient input. Some of the species evaluated here can be included into the third group; and others into the first group if the interval between disturbances is long enough as was reported from central Europe by Krahulec, Lepš et Rauch (1980), Prach (1987), and Osbornová et al. (1989). There is the substantial increase of frequency of these habitats in many regions of Europe. An expansion of species adapted to the respective habitat types is a consequence of this. The groups of species mentioned above can be related to some extent to Grime's R, S-R, and C-R strategists, respectively (Grime 1979).

The evaluation of the species in Table 1 is weighted in favour of certain criteria and probably discriminates against others. The importance of qualitative characteristics can be underestimated. For example, self-compatibility is expected to be very important in the expansion behaviour of a species (see Bazzaz 1986). Unfortunately, it was not possible to reasonably quantify the range of environmental conditions suitable for germination, though it can also be a decisive trait for expansion (Roy 1990). On the other hand, the perennial habit does not appear to be so important for a species to be a successful weed or expansionist as illustrated by annuals like *Impatiens parviflora, I. glandulifera,* and *Bidens frondosa.* Further research is necessary to substantiate the weighting. As traits crucial for expansive behaviour, we consider those concerning the species regenerative strategy (sensu Grime, Hodgson et Hunt 1988), i.e. productivity

and dispersibility of generative diaspores combined with intensive vegetative spreading, to be the most important. Species which possess this ability can be very successful in expansion unless any relevant limitation operates.

Results from Table 1 are commented on in the next section with respect to the individual species. Examples on their behaviour in Czechoslovakian landscape are given.

Comments on the species

Agropyron repens (L.) Beauv. is one of the most pernicious weeds, common also in many ruderal sites such as coal mining dumps (Prach 1987), abandoned fields (Osbornová et al. 1989), and urban habitats (Pyšek et Pyšek 1988). The outstanding ability for vegetative spread and its propensity for regeneration even from small fragments of rhizomes are the most important traits responsible for expansion. This compensates for the comparably low seed production and dispersibility. For other information on the species see, in particular, Werner et Rioux (1977), Grime, Hodgson et Hunt (1988).

Artemisia vulgaris L. and *Tanacetum vulgare* L. exhibit similar ecology, colonizing various mesic and slightly xeric disturbed sites. In these situations they form typical stages which succeed the earlier stages of annuals and biennials. Their regeneration strategy is also similar. They produce large numbers of tiny seeds easily dispersed despite the lack of pappus. In contrast to other species reviewed here, vegetative spreading is not so relevant in these species.

Baldingera arundinacea (L.) Dum. is the most expansive species in central European wetlands (for an example of its expansion see Šrůtek et al. 1988) being encouraged by increasing nutrient input. Its behaviour is similar to *Urtica dioica*, however, its ability to grow well under very wet conditions is pronounced. The species is less susceptible to regular mowing than *U. dioica* (Piňosová in Šrůtek et al. 1988). Transport of rhizomes and fragments of shoots by water is very important for the expansion as well as establishment by seeds. The compact cover of the species can inhibit further successional changes. For other characteristics of the species see Grime, Hodgson et Hunt (1988).

Calamagrostis epigeios (L.) Roth can be considered to be the most expansive species in the Czechoslovak landscape in various disturbed sites. It exhibits extremely broad ecological amplitude, growing from littoral zones of aquatic habitats to dry, steppe sites. Diaspores are often sterile (Dolečková 1988), however, their great production and efficient dispersal enable the species to establish even in distant places. The high competitive ability is largely supported by production of compact litter which decays very slowly (Dolečková 1989, Osbornová et Dolečková 1990, Prach, unpublished data). The species is rarely succeeded by any other in spontaneous succession, and it is hardly suppressed by artificial measures (Dolečková 1988). Continuous expansion of this species is expected.

Chamerion angustifolium (L.) Holub has an extremely high seed production (maximally more than 1 million per square meter per year) and possesses highly

efficient dispersal mechanisms (Prach 1988) giving great advantage to this species in colonizing even very distant, disturbed sites. For other details see Grime, Hodgson et Hunt (1988).

Cirsium arvense (L.) Scop. has a strategy similar to *Agropyron repens*, and in addition, exhibits higher seed production and dispersibility. The dispersibility is potentially very high (Moore 1975, Prach 1988), however, the pappus can be easily detached from the seed and this reduces its effective dispersal. For other details see Moore (1975).

In *Tussilago farfara* L. the combination of efficient seed dispersal and intensive vegetative spread is, again, predominantly responsible for the success of this species in disturbed landscapes. Seed dispersal early in the season (April-May), followed by rapid growth, can be advantageous in the rapid colonization of new, open sites before other species. For other characteristics see Ogden (1974) and Grime, Hodgson et Hunt (1988).

Typha angustifolia L. and *T. latifolia* L. do not differ remarkably in their population characteristics (see Grace et Harrison 1986) and are thus considered together. They are probably two of the species with the highest seed production and most efficient dispersal ability. However, their expansion is limited by their comparably narrow ecological amplitude. Colonization and expansion are restricted to open wet sites, usually in newly created reservoirs and water pools (Krahulec, Lepš et Rauch 1980). Moisture is an especially limiting factor in germination (Grace et Harrison 1986). For other species characteristics see Grace et Harrison (op. cit.).

Urtica dioica L., in this evaluation, was the species with the highest expansion ability. However, stinging nettle hardly grows on poor, dry, and excessively wet sites, and is susceptible to regular disturbance like mowing. Thus, the expansion is limited to certain types of habitats: ill-managed wet meadows, especially in floodplains, alluvial forests, wet dumps of organic material, margins of wetter fields, etc. In all cases, high nutrient level is the decisive factor enabling the species to expand (Šrůtek et al. 1988). Considering population characteristics, prolonged viability of seeds and intensive vegetative spread are important features for the continuous expansion of this species. For other details on the species see Bassett, Crompton et Woodland (1977), Grime, Hodgson et Hunt (1988), Šrůtek et al. (1988).

Expansion of species is generally determined by (a) character of a species, (b) availability of a species in a landscape, (c) character of sites where a species can potentially expand, and (d) frequency of the sites in a landscape. In this article, we examined only some population characteristics belonging to (a), and generally considered the high availability of the species in the landscape (b). For more reliable prediction of expansion of these and other species, the examination of the site characteristics, i.e. (c) and (d), is necessary, together with further studies of the population ecology and autecology of the species. For the more advanced evaluation, some other species traits can also be quantified, see Bazzaz (1986), Grime, Hodgson et Hunt (1988), and Roy (1990).

Acknowledgment

We thank P. Pyšek for his comments on the manuscript.

Souhrn

Vytrvalé druhy bylin domácího původu, výrazně se šířící ve středoevropské krajině, byly hodnoceny pomocí upravených Bakerových charakteristik "ideálního plevele" (Baker 1965). Byly shromážděny převážně literární údaje o maximální relativní růstové rychlosti (RGR_{max}), podmínkách klíčení, časnosti první generativní reprodukce, schopnosti samoopylení, produkci generativních diaspor, jejich šíření v prostoru a udržení jejich životaschopnosti, intenzitě vegetativního šíření a o maximální výšce rostlin jako nejjednodušším ukazateli kompetiční schopnosti druhu. Tyto charakteristiky byly hodnoceny jednoduchými semikvantitativními stupnicemi nebo jako kvalitativní znaky. V následujícím přehledu jsou druhy, které byly zahrnuty do analýzy, seřazeny podle klesající expanzívní schopnosti, jak byla ohodnocena výše uvedeným postupem: *Urtica dioica; Cirsium arvense; Typha angustifolia/latifolia, Chamerion angustifolium, Artemisia vulgaris, Baldingera arundinacea; Calamagrostis epigeios; Tanacetum vulgare; Agropyron repens, Tussilago farfara*. V závěru jsou komentovány jednotlivé druhy s ohledem na jejich skutečnou nebo potenciální expanzi.

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Received 14 February 1991
Accepted 4 September 1991

L h o t s k á M., K r i p p e l o v á T. et C i g á n o v á K.

Ako sa rozširujú rastliny

Obzor, Bratislava 1987, 392 str., 13 čb. a 258 barev. obr., 1 tab., 242 barev. foto, 2 mapy. [Kniha je v knihovně ČSBS.]

M. Lhotská, dlouholetá pracovnice v oboru karpobiologie a diasporologie rostlin, připravila ve spolupráci s T. Krippelovou a K. Cigánovou zajímavou vědecko-populární knihu, věnovanou otázkám rozmnožování a rozšiřování rostlin.

Kniha je rozdělena na všeobecnou a speciální část. V prvé z nich jsou vysvětleny obecné pojmy, spojené s uvedenou problematikou. Sem je též zařazena stať o klíčení a klíčním odpočinku rostlin. Autorka textu M. Lhotská včlenila do knihy formou přístupnou široké veřejnosti výsledky svých dlouholetých terénních pozorování a laboratorních pokusů. Jednotlivé způsoby rozmnožování nebo rozšiřování rostlin dokládá řadou názorných příkladů, zdařilými fotografiemi T. Krippelové i názornými obrázky K. Cigánové, zhotovenými podle živého materiálu.

Ve speciální části knihy jsou podrobně analyzovány různé způsoby rozmnožování a rozšiřování. Zde se autorky zaměřují na jednotlivé rostlinné rody a druhy naší domácí i ruderální flóry. Po krátkém popisu jednotlivých taxonů následuje stručná chrakteristika jejich přirozeného výskytu a stanovištních nároků a podrobné údaje o způsobu jejich reprodukce. Ze způsobu rozšiřování mnohých druhů je patrná úzká vazba mezi rostlinnou a živočišnou složkou biocenózy. Z uvedených příkladů mohou též čtenáři posoudit výrazný vliv člověka na složení flóry a vegetace různých oblastí.

Knihu doplňuje stručný terminologický slovník a seznam slovenských, českých a latinských názvů rostlin.

Tato poutavá a přehledně uspořádaná publikace je určena širokému okruhu čtenářů. Přináší četné podněty k prohlubování znalostí o přírodě a dějích v ní probíhajících. Z tohoto důvodu ji lze doporučit zejména mladým adeptům botaniky.

Z. N e u h ä u s l o v á