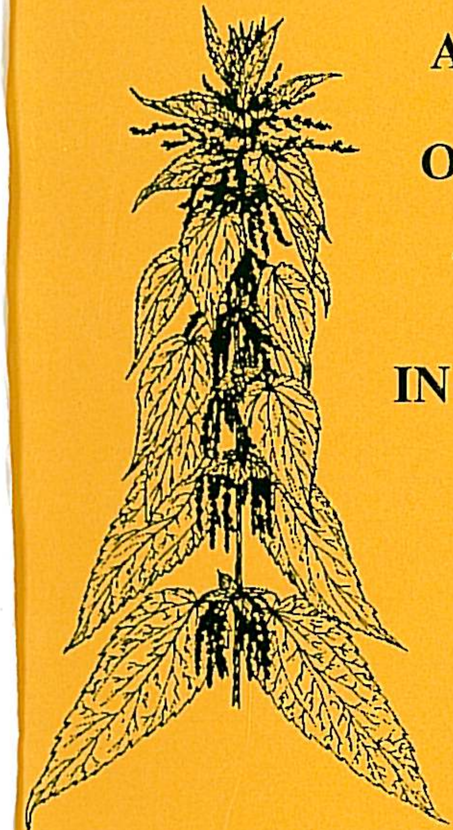
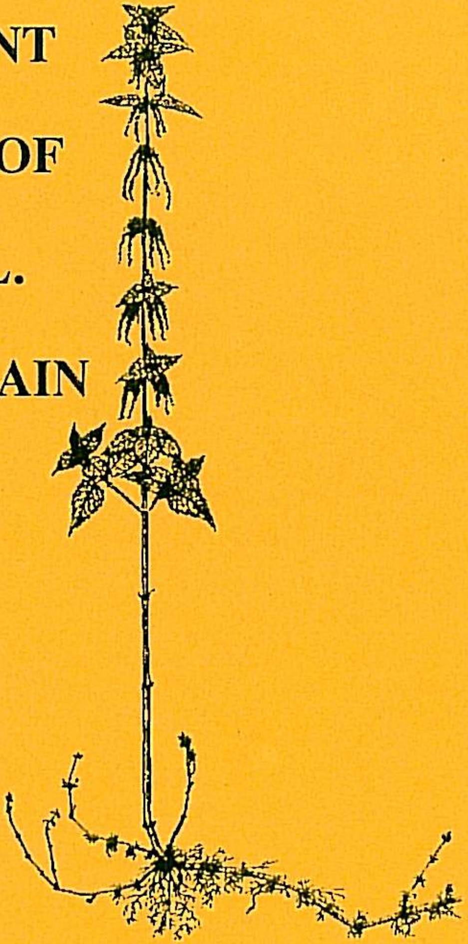
THE FACTORS
AFFECTING GROWTH
AND DEVELOPMENT
OF POPULATIONS OF
URTICA DIOICA L.
IN RIVER FLOODPLAIN





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THE FACTORS AFFECTING GROWTH AND DEVELOPMENT OF POPULATIONS OF *URTICA DIOICA* L. IN RIVER FLOOPLAIN

Dissertation
in Faculty of Biological Sciences, University
of South Bohemia

by
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České Budějovice, March 1995

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PREFACE

The study was iniciated by Prof. Jan Jeník, Department of Botany, Charles University, Prague (until 1991 Institute of Botany, Dept. Plant Ecology, Třeboň). He was a head of the synecological group in Třeboň and he iniciated, together with Karel Prach, the ecosystem project "Upper Lužnice River" (see "General introduction"). Besides *Urtica dioica* study, population ecology of several other plant species (e.g, *Rumex obtusifolius* agg., *Phalaris arundinacea, Carex gracilis, Carex rostrata, Carex vesicaria, Calamagrostis canescens*, and selected willow species) were studied by my colleagues.

Acknowledgements are often rather formal. On the other hand, it is evident that it is impossible to finish any work without help, advice and discussions with colleagues and friends.

I thank you very much to Prof. Jan Jeník who was one of my most important teacher of botany.

I frequently remember discussions with my colleague and friend Leoš Klimeš which were very important, particularly for establishment of my experiments. Therefore, I thank him very much.

My patient supervisor and friend Jan Šuspa Lepš is probably glad that I have finished my thesis because he spent much time with me discussing particularly statistical problems. I thank him very very much.

Greatest thank belongs to my wife. It would be impossible to finish my work without her tolerance.

FAKTORY OVLIVŇUJÍCÍ RŮST A VÝVOJ POPULACÍ *URTICA DIOICA* L. V ŘÍČNÍ NIVĚ

Studium populační ekologie *Urtica dioica* (kopřivy dvoudomé) bylo zadáno jako součast ekosystémového výzkumu nivy řeky Lužnice. Tento komplexní projekt byl zaměřen na studium struktury a dynamiky vybraných prvků nivy malé řeky a probíhal v letech 1986-1993. Centrem výzkumu byla příhraniční část řeky Lužnice a její niva ("Horní Lužnice") mezi hranicí s Rakouskem a obcí Suchdol nad Lužnicí v biosferické reservaci Třeboňsko. Vedle studia ekosysytému říční nivy a mokřadních společenstev, byly studovány jednotlivé rostlinné i živočišné organismy a jejich populace (Drbal et Jeník 1988).

Kopřiva dvoudomá jako dominantní expanzivně se šířící druh nemohl být při studiu organismů opomenut. V současné době, zejména v posledních letech chudých na srážky a tedy na pravidelné záplavy se tento druh rychle šíří. Rozsáhlé porosty tvoří zvláště v místech, kde není niva dlouhodobě kosena (Šrůtek 1993). Její expanzivní šíření je podporováno i značným přísunem živin přinášených řekou a splavovaných do nivy z okolních polí.

Doktorandská práce byla zaměřena zejména na studium vlivu vybraných abiotických a biotických faktorů, které byly považovány z hlediska růstu a vývoje populací kopřivy za nejvýznamnější. Jedná se o následující faktory: 1) abiotické - obsah živin v půdě a hladina podzemní vody, 2) biotické - kosení, vnitrodruhová konkurence. Mimo vlivu kosení (experimentální data jsou zpracovávána) jsou výsledky studia uvedených faktorů součástí předložené práce. Součástí je též srovnávací studie o struktuře podzemních orgánů *Urtica dioica* a *Phalaris arundinacea* (lesknice rákosovité).

Úvodní kapitola shrnuje znalosti o biologii kopřivy a je koncipována jako literární přehled většiny dostupných prací. Studie o rozšíření kopřivy v nivě řeky Lužnice je především charakteristikou ruderálních rostlinných společenstev s dominující kopřivou a lesknicí v příhraniční části nivy. Práce byla již publikována (Vegetatio, Dordrecht).

Další dvě studie řeší problematiku vlivu různého obsahu živin v půdě a různé hladiny podzemní vody na růst a vývoj populací kopřivy. Kapitola 3. je přijata do tisku

(Canadian Journal of Botany, Vancouver) a kapitola 4. byla odeslána do redakce časopisu (Acta Oecologica, Montrouge Cedex)

Studium vnitrodruhové konkurence bylo založeno na velice přínosné spolupráci s dr. T. Harou (Tokyo Metropolitan University, Japan), který v dané problematice uznávaným odborníkem. Práce je nyní v recenzním řízení (Annal of Botany, London).

Studium vertikálního rozložení podzemních orgánů *Phalaris arundinacea* a *Urtica dioica* bylo iniciováno společnou prací na dominantních druzích vyskytujících se v nivě řeky. Dr. J. Klimešová se v rámci aspirantského studia zabývala též výzkumem populační biologie lesknice rákosovité (Klimešová 1993). Práce je přijata do tisku (Preslia, Praha).

Práce byla, jako součást grantu dr. L. Papáčkové "Invazní šíření rostlinných populací v důsledku eutrofizace", podporována Grantovou agenturou ČSAV. Společný pokračující projekt s dr. T. Harou je finačně dotován japonskou grantovou organizací (Japan Society for the Promotion of Science).

chapter 1

GENERAL INTRODUCTION

GENERAL INTRODUCTION

The present thesis represents a part of the project Upper Lužnice River carried out by the Department of Plant Ecology, Institute of Botany, Třeboň during 1986-1993. The project was based on the ecosystem approach and focused upon ecological processes in the small river and its floodplain (Drbal et Jeník 1988).

The upper part of the Lužnice River flows through the Třeboň Basin, South Bohemia, Czech Republic. The river section considered by the project was that between the Czech-Austrian border (14° 57' E, 48° 48' N; near the village of Nová Ves nad Lužnicí) and the town of Suchdol (14°53' E, 48°53' N), i.e. between 149 and 126 river kilometers. The area studied is an example of a wetland strongly influenced by humans. The longer section of the river is relatively undisturbed, with meanders and riparian woody and scrub vegetation. The short section, near Suchdol, has been channelized. The floodplain varies in width approximately from 80 to 650 m (Šrůtek 1993).

Geological substratum of the floodplain consists of two to three Pleistocene terraces from the Riss and Würm periods (Chábera et al. 1985). Mean annual temperature is 6.6 °C, mean annual sum of precipitation equals 627 mm (50-years average, Třeboň meteorological station - 433 m a.s.l., Prach et al. 1990).

A diverse set of wetlands has developed in the river floodplain along streams, canals and fishponds, depending on the dynamics of water table. Those parts which are being used less intensively harbour various types of natural and seminatural vegetation, e.g. tall-graminoid marshes (class *Phragmiti-Magnocaricetea*), fragments of short graminoid communities (cl. *Scheuchzerio-Caricetea fuscae*), productive meadows (alliances *Alopecurion* and *Calthion*. The river is fridged by willow scrubs (e.g. all. *Salicion triandrae*). Some segments of the floodplain are covered by swamp-alder communities (all. *Alnion glutinosae*). Large areas on terraces, originally covered by mixed and deciduous woodlands, are nowadays used for forest plantations, usually dominated by *Pinus sylvestris* (Moravec et al. 1983, Ellenberg 1988, see Prach et al. 1990 for details).

The systematic human colonization of the Třeboň Basin started as late as in the 12th century (Jankovská 1980). The neighbouring Austrian part of the basin has been strongly modified by human impact since about 1,000 A.D. (Ricek 1982). However, great changes in meadow and wetland management have taken place in the Czech part of the Třeboň Basin during the last 30-40 years, and as a part of the area, the floodplain was also strongly affected (Šrůtek 1993).

Extensive areas had been transformed into intensively used permanent grasslands, with artificially sown grass species playing an important part in the composition of communities. On the other hand, the wetter parts of the floodplain were abandoned, i.e. left without any management at all. Consequently, original wetland vegetation of the abandoned sites had changed into wet ruderal stands, often dominanated by *Phalaris arundinacea* and *Urtica dioica*, i.e. species capable of forming poor monospecific stands. Particularly, the latter species has been spreading dramatically during the last several years, its expansion being encouraged by the low frequency of floods (Prach 1992, 1993, 1994). Striking changes in species composition are also evident in intensively manured (particularly by piggery sewage) regularly mown meadows (Šrůtek 1993).

The first historical records of *Urtica* from sites of anthropogenous origin in the Třeboň Basin comes in Post-Glacial period from the younger Subatlantic (1,000 A.D.) (Jankovská 1983) but the spread of the species accelerated remarkably in the several last decades, and particularly the Lužnice River floodplain has been suffering from its expansion (Šrůtek 1993).

Research objectives

The present thesis was focused upon the ecology of *Urtica dioica*, one of the most common species of the floodplain (Šrůtek 1993). Being a dominant component of vegetation in a large part of the study area, the species may be supposed to affect principally the ecosystem functions of the floodplain.

The study was aimed at recognizing those factors affecting in a decisive way the growth and development of *Urtica* populations in the Lužnice River floodplain. Both (1) abiotic (soil nutrients, groundwater table dynamics) and (2) biotic factors (intraspecific competition) were considered.

The effects of changes in groundwater table levels and those of nutrient conditions were studied by garden and greenhouse experiments, respectively. The other factors were analysed in the field using permanents plots. Furthermore, the distribution of *Urtica* stands in selected segment of the Lužnice River floodplain was recorded and their relationship to landscape management was investigated.

The study was supported by the grant No. 60539 of the Czech Academy of Sciences "Invasive plant populations in eutrophic habitats" and by the grant of the Japan Society for the Promotion of Science "Growth dynamics of grassland plant communities with *Urtica, Festuca* etc. in Europe".

Outline of ecology of Urtica dioica

Urtica dioica *as a study subject*

Urtica dioica L. (stinging nettle) is a frequent subject of population ecological studies, especially in Anglo-Saxon coutries and Germany. The research effort invested into the species makes it comparable with such frequently investigated species as *Trifolium repens, Ranunculus repens, Glechoma hederacea, Solidago altissima, Agropyron repens, Plantago lanceolata* and *Lolium perenne* (Harper 1977, Hutchings et Bradbury 1986, Grime et al. 1989, Hendry et Grime 1993). There are about one hundred papers available dealing with some aspect of autecology and/or population ecology of *Urtica dioica* s.l.

Distribution

Urtica was recognized already 3,000 years B.C. in neolithic buildings in Switzerland. It was frequently used as a tissue plant and numerous papers on its cultivation since the 19th century have been published (Bredemann 1959). However, the first reports about its practical importance were recognized even earlier. For example, the Russian monk Nestorius (900 years A.D.) mentioned excellent-quality ship ropes, mainsails and cloth produced from nettle fibre (Bredemann 1959).

Urtica dioica, native to Euroasia, at present occurs all over the world (Hultén et Fries 1986) except of tropical regions (Grime et al. 1989). It is widespread and probably native throughout Europe and Asia from the Mediterranean to the Arctic regions and naturalized in other temperate regions of the world (India, China, Australia, New Zealand, N and S Africa and N and S America; e.g., Hashimoto 1982).

The species is common on the whole territory of the Czech Republic from lowlands to mountains, penetrating into subalpine belts. The altitudinal maximum was reported from the Sněžka Mt. at 1603 m a.s.l. (Slavík 1986, Hejný et Slavík 1988).

Taxonomy

The chromosome number 2n = 52 was found in Czech populations of *Urtica* (Měsíček et Jarolímová 1992) but reports on different numbers (2n = 32, 48) do exist as well (Pollard 1981). *Urtica* is very variable species, particularly in vegetative parameters (branching, color, shape and size of leaves; Hejný et Slavík 1988, Geltman 1986) and probably containing a number of subspecies (Tutin et al. 1964). Numerous intraspecific taxa have been described but their taxonomical value appears to be disputable (Hegi 1957). Pollard et Briggs (1982, 1984) stressed the importance of phenotypic plasticity in *Urtica* and concluded that much of the intraspecific variation is genetically based and therefore heritable.

Van Damme et Peumans (1987) gave an evidence for phenotypic plasticity among 102 clones of *Urtica* in Belgium. By analysing agglutinin from *Urtica*, they found that this lectin was a complex mixture of isolectins, and at least 11 different isolectins could be traced.

Phytosociology and species richness

In central Europe, vegetation with *Urtica* has been a frequent subject of traditional Braun-Blanquetian classification (Braun-Blanquet et Tüxen 1943, Klika 1955, Passarge 1967, Kopecký 1969, Dierschke 1974, Hadač 1984, Meβner 1985, Klotz et Köck 1986, Bastian 1987, Uherčíková 1989, 1991 and others). The communities with *Urtica* are being classified into the following higher units:

(1) Natural vegetation with more or less frequent occurrence of *Urtica*: classes *Salicetea purpureae* Moor 1958 (willow communities on floodplains) and *Alnetea glutinosae* Br.-Bl. et Tüxen 1943 (alder swamp woods and mire willow scrub), from class *Querco-Fagetea* Br.-Bl. et Vlieger in Vlieger 1937 alliances *Alno-Ulmion* Br.-Bl. et Tüxen ex Tchou 1948 em. Th. Müller et Görs 1958 (alder

and noble broadleaved woods of floodplains), *Tilio-Acerion* Klika 1955 (mixed maple woods and maple-beech woods) and *Rubo-Prunion spinosae* (Tüxen 1952) Th. Müller in Oberdorfer et al. 1967 (blackthorn scrub) (Moravec et al. 1983, Ellenberg 1988).

(2) Synanthropic and ruderal vegetation (i.e. that on man-made sites) with *Urtica*: class *Galio-Urticetea* Passarge ex Kopecký 1969 (natural and anthropogenous communities of perennial herbs on the moist and slightly drying sites) (Hejný et al. 1979, Ellenberg 1988, Kopecký et Hejný 1992).

In the Lužnice River floodplain, the river banks are occupied by willows whereas alder swamp woods and mire willow scrub (class *Alnetea glutinosae*) form small woods further from the river flow. The mixtures of various herbaceous and grass species with *Urtica* as well as almost monospecific stands of *Urtica* in unshaded sites can be ranked into the class *Galio-Urticetea*. The latter stands have very low species diversity, reflecting the strong competitive ability of the dominant species. Only a few species are capable of persisting in such stands, e.g. *Ficaria verna, Anemone nemorosa* (these two species benefit from the geophyte life form and prevail in spring), *Galium aparine, Glechoma hederacea, Phalaris arundinacea, Cirsium palustre, Ranunculus repens* and *Angelica sylvestris*. Šrůtek (1993) documented the changes in species richness of *Urtica* stands in different parts of floodplain exposed to different management. The nettle stands on the margin of mowed meadows under the riparian shrubs and trees were richer in species than those in open flooplain. Species number in 215 vegetation samples ranged from 1 to 23 and depended principally on *Urtica* cover.

In an experiment conducted in a former orchard, van der Maarel (1980) found a rapid increase of *Urtica* after fertilization, accompanied by a rapid decrease in species number.

Habitats

Urtica dioica prefers open habitats (floodplains, pastures, meadows) and represents a species typical of moderately shaded woodlands (Wheeler 1981, Reif et al. 1985). It occurs on almost all soil types, though absent from waterlogged soils (Greig-Smith 1948). Floods significantly reduce the survival of young plants. Unless the inundation is long or permanent, the effect on older plants is never such strong, resulting only in their lower biomass (Klimešová 1994). Grootjans et al. (1985) emphasized that lowering of the groundwater table level in wet meadows lead to a sharp increase of nitrophilous grassy vegetation with ruderal species such as *Cirsium arvense, Urtica dioica, Stellaria media,* and *Athriscus sylvestris.*

Grime et al. (1989) provided a complete overview of habitats occupied by *Urtica* and pointed out that on fertile soils, the species persisted under moderate shade whereas on arable land and in other highly-disturbed habitats it usually occurs as isolated seedlings. Generally, the species is most successful in fertile, relatively undisturbed sites. Occasionally, it also occurs as an epiphyte on willow, ash, hornbeam, oak and poplar trees (Greig-Smith 1948).

Various authors emphasized the man-induced spread of *Urtica* in Europe (Rijmenans 1984, Roberts et Boddrel 1984, Ellenberg 1988, Grime et al. 1989), mainly in ruderal sites (rubbish heaps, construction sites, surroundings of mountain chalets, roads ditches etc.; Rebele 1992, Šrůtek 1993). Schmidt (1981) suggested that *Urtica* often forms tall monospecific communities on ruderal sites rich in nutrients and water. Greig-Smith (1948) called the species "an almost universal follower of man".

In the Lužnice River floodplain, the original occurrence of *Urtica* was probably restricted to river banks. However, its present occurrence ranges from several-shoot patches (often representing a single clone) to the stands covering up from several ares to hectare. The spontaneous secondary succession in many places of the floodplain thus leads to the dominance of *Urtica* stands of which may persist for many years (Šrůtek 1993).

Mineral nutrition and nutrient dynamics in the tissues of Urtica

In his classical paper, Olsen (1921) pointed out that *Urtica* requires nitrogen supplied in the form of nitrate. Nitrates are found particularly in aerial stems, rhizomes, and roots, but in smaller quantity in leaves as well. He suggested that the nitrifying power of the soil is the factor controlling the species occurrence (see also Greig-Smith 1948, Ivins 1952, Walter 1963, Holter 1979 etc.). The species' high demands for mineral nutrition and its preference for nitrogen-rich sites was also reported by Rijmenans (1984) and Reif et al. (1985). Ivins (1952) recorded *Urtica* in plots originally sown with legume species which increase the content of organic nitrogen in the soil. However, Bates (1933), pointed out that the physical features of the substratum also control the species occurrence.

Pigott et Taylor (1964) suggested that *Urtica* is limited by the concentration of phosphate in the soil and not by nitrogen content. Similarly, Pigott (1971) concluded that *Urtica* is strongly limited by very low concentration of phosphates in the topsoil of woodlands. Holter (1979) precised that the phosphate level, though only on some sites (e.g. wasteland), was so low that it limited the species distribution, whereas in roadsides it was sufficient and other factors were limiting. Abeyakoon et Pigott (1975) considered the substratum type and phosphate form as very important for the growth of *Urtica.* They planted seedlings of several species, including *Urtica,* on soil from the upper horizons of uncultivated rendzina and on brown forest-soil. On both soils, all species responded to the addition of soluble phosphate. However, there was no response to the addition of apatite on the rendzina, whereas on the brown forest-soil, the response to apatite was as remarkable as that to the soluble phosphate. *Urtica* grew also in sand-culture with additional soluble phosphate but did not respond to the presence of humus which is rich in organic phosphate. Hruška (1987) stressed that common nitrophilous species such as *Urtica dioica, Parietaria officinalis, Artemisia vulgaris* etc. start to develop in response to the increase of organic substances in the soil. Rorison (1968) pointed out that *Urtica* showed very poor growth on nutrient solution with low phosphate concetration.

The growth curves reported by Rorison (1968) confirmed that *Urtica* and *Rumex acetosa* had high relative growth rates which respond markedly to changes in external phosphorus concentrations. The greatest growth rate for *R. acetosa* was reach at around 10^{-3} M of phosphorus concetration but for *Urtica* it was above 10^{-3} M.

Availability of nutrients, including nitrogen, is affected also by soil moisture and pH. Reif et al. (1985) and Hempeling et al. (1988) documented that on moist and nitrogen-rich soils (e.g. in penumbra of deciduous forests) *Urtica* produced taller shoots than on dry soils and in sunny sites. This may be presumably explained by water deficiency and higher allocation of nitrogen into flowers and fruits on the debt of vegetative tissues. On the same vein, Šrůtek (1993) demonstrated a close relationship of *Urtica* to moist and nutrient-rich habitats. According to Grime et al. (1989) the species has high frequency and abundance on soils with pH between 5.0 and 8.0.

Hofstra et al. (1985) investigated the nitrogen dynamics in tissues during the growth of *Urtica* plants using two nitrogen assimilating enzymes, nitrate reductase and glutamine synthetase. Shoot growth was retarded at low nutrient supply but this was not true for root growth. The comparison with less nitrophilous *Plantago lanceolata* showed that at 100 % nutrient supply there was a correlation between nitrate reduction and glutamine synthetase activity in that part of the plant which exported the reduced nitrogen, i.e. the root in *Plantago lanceolata* and shoot in *Urtica dioica.*

The high nutrient supply was shown to shift assimilate partitioning toward producing more leaves (even after the maximum leaf area index is reached) and permanent abscission of leaves occurs due to self-shading, which is a phenomenon observed in *Urtica* stands in the wild (Teckelmann 1987). *Urtica* builds a dense canopy as early as at the stage of seven green expanded leaves, but plants continue to produce new leaves. Continual leaf production and abscission lead to the total leaf canopy being replaced about three times during a growing period. Despite a retranslocation of about 60 % of nitrogen, the leaf nitrogen pool must be replaced two times from the soil during each growing season. Given the biomass of *Urtica* leaves about 0.5 $kg.m^{-2}$, 20 $mg.g^{-1}$ of total nitrogen are lost in the litter so that almost 30 $g.m^{-2}$ of nitrogen are returned to the chain of decomposers during the growing period (Schulze et Chapin III 1987, Teckelmann 1987).

Rosnitschek-Schimmel (1982) pointed out that shoot/root ratio increased with increasing nitrogen supply. The lack of nitrogen did not affect the enhanced root growth which takes place indirectly via the sugar balance of the plant.

The high accumulation of nitrogen-rich amino acids, asparagine and arginine, in belowground organs (roots and rhizomes) of *Urtica* is known. This points to possible role of these free amino acids in the detoxication of abundant NH_4 and as storage and transport of nitrogen (Rosnitschek-Schimmel 1983). The highest concentrations of arginin are found in overwintering roots and rhizomes of *Urtica*, representing the major nitrogen storage. In this respect, the high concentration of arginin found in the shoot may be seen in terms of transport from the leaves to the roots (Rosnitschek-Schimmel 1982).

Gebauer et al. (1988) documented the contents of nitrate and organic nitrogen as well as the nitrate reductase activity in individual organs of many European plants. *Urtica* had the highest content of nitrate in shoot axis, including petioles. The organic nitrogen was highest in leaves or reproductive organs, depending on a site. The nitrate reductase activity was highest in leaves. Rosnitschek-Schimmel (1983) noted that *Urtica* belongs to those plants reducing nitrates only in leaves and found thus about 98 % of the total nitrate reductase activity in these tissues (see also Al Gharbi et Hipkin 1984).

Urtica is able to accumulate heavy metals in plant tissues. For example, Otte et Wijte (1993) reported that the high metal concentrations in roots of *Urtica* in the pure reed habitat coincide with NaOAc (Cd, Cu, Zn), NH_4OAc (Cu, Cd) and H_2O (Zn) extractable metal fractions, and the same is true for low metal concentrations in grasslands which were investigated.

Phenology

The young shoots of *Urtica* are produced both in autumn and in spring. The autumnal shoots may overwinter but some are killed. The spring (April) and autumn (October) density of shoots was 400-700 and 100-200 per sqm, respectively, which means that the shoot mortality during the growing period is rather high (65-80 %; Šrůtek, unpublished data). The peak in biomass production occurs at the end of July (Al-Mufti et al. 1977). Flowers period is from June to July and seeds are shed from August onwards (Grime et al. 1989).

Floral and fruit morphology and biology

Urtica dioica is wind-pollinated. When the anthers are mature the stamens straighten explosively, scattering the pollen. Insect pollination may also occur occasionally. Inflorescences sometimes bear a few hermaphroditic flowers or those of the opposite sex (Greig-Smith 1948).

Flowering is strongly inhibited by drought. The process of drought hardening has been described and coincides with growth reduction and delay in flower production. This represents the mechanism of survival and possible reproduction known for long-lived species capable of exploiting productive, relatively undisturbed habitats (Boot et al. 1986).

Fruits are single-seeded. Both the fruits and other parts of reproductive organs may adhere to clothes by persistent perianth, dropping off as they become dry (Greig-Smith 1948). The seed is oval-shaped achene, 1.3 x 1.0 mm in size and 0.19 mg in weight (Hejný et Slavík 1988, Grime et al. 1989).

The growth of perianth (calyx and corolla) and its differentiation is finished during the last stages of fruit ripening and drying off, after the development of the other covers of fruit and seed has been completed. Seed cover morphology differs among *Urtica* species in the form and dimensions of perforation. Species differences also exist in the distribution of pigments in the cover of fruit and seed (Kravtsova 1993).

Seed ecology, seedling establishment and vegetative propagation

Only a limited information is available on seed production in *Urtica*. To my knowledge, the only figures are those by Bassett et al. (1977) who assessed the fecundity of *U. dioica.* subsp. *gracilis* from Canada, and found 10-20,000 seeds per shoot in open areas and have 500-5,000 in shaded habitats. Habitat differences in seed production were also found by others (Al-Mufti et al. 1977, Wheeler 1981).

As to the seed bank, Wheeler (1981) reported on 88-1,664 viable seeds per sqm in woodlands, and 1,754-9,090 in pastures.

Large persistent seed bank in a semi-natural grassland was found by Milberg (1992) who investigated the number of *Urtica* seedlings in sand soils as well. The values ranged between 0.64 and 59.6 per sqm depending on the type of management (mowing, fertilization).

Hutchings et Russell (1989) studied the seed bank in an emerged salt marsh. *Urtica* seeds contributed substantially to the total number of seeds recovered in all experimental sites but the cause of the sudden and sustained appearance of seeds in the seed bank was unknown.

Relatively rapid decrease in the soil seed bank of several weeds of arable land (including *Urtica*) following set-aside management (i.e. sowing of grasses in previously intensively managed field) was documented by Lawson et al. (1992).

The seeds of *Urtica* can remain viable for long (Ødum 1978). In the greenhouse, the seeds may germinate after 10 year storage (Bassett et al. (1977). In contrary, Roberts et Boddrell (1984) found the seeds of *Urtica* in cultivated soil being relatively short-lived, and of the 3% of seeds which on average remained viable after 5 years.

Ripe seeds are being shed approximately from the end of August and often remain on the plant until frost (Bassett et al. 1977). Water is the most common dispersal agent in *Urtica* in riparian habitats, although occassional endozoochory was also reported by Pijl (1982) who found the seeds in the faeces of cattle, fallow deer and magpie. The seeds survive ingestion by a variety of animals and may be carried to a long distance (Greig-Smith 1948). Ectozoochory and anthropochory are also common ways of dispersal. Seeds and rhizome pieces are also transported with soil and, for this reason, the species is highly mobile despite of the lack of a well-defined dispersal mechanism (Grime et al. 1989).

Seed dormancy is up to 3-5 months and under the light/20 °C temperature regime, germination starts after about ten days. In the year following the seed collection, 50-70 % germination was found from March to September, decreasing to 10 % in October. An increase in germination rate followed in February of the following year (Nikolaeva et al. 1985). The seeds do not require vernalization (Bassett et al. 1977).

The species has epigeal germination. Half of the seed set germinated in 22-35 °C (representing upper and lower limits of the temperature range in the wild) during six days following the inbibition of air-dried seeds. Germination is inhibited by darkness and stimulated by light and fluctuating temperature, occuring thus mainly on open and disturbed ground. The sites with dense vegetation cover are unfavourable for the regenaration by seed (Grime et al. 1989).

Pigott (1971) showed a small percentage of seeds still germinate at 0.01 % daily irradiance and concluded that light induction is through a phytochrome mediated system.

Seeds collected directly from *U. dioica* subsp. *gracilis* plants germinated in 5-10 days (Bassett et al. 1977).

On pastureland, the germination starts in early January and the peak is reached in March, at the mean temperature of 13-15 °C and daily fluctuations of 5 °C. It was restricted to bare ground where the favourable spectral composition of light and temperature fluctuation trigger the germination of seeds deposited on the soil surface. In woodlands, the onset of germination was in the first half of March, coinciding with the peak of breakdown of the leaf litter (Wheeler (1981).

According to Klimešová (1995), the germination and seedling establishment of *Urtica* in the floodplain are limited by the lack of light mainly in dry period. The suitable sites for seedling establishment were erosion rills, newly sedimented sand or detritus drifts emerged. Also mowing, as a regular disturbance, encouraged the germination and seedling establishment in the floodplain. She emphasized that the youngest seedlings of *Urtica* survived the spring flood, and their post-flooding mortality might have been caused by post-anoxic injury (Klimešová 1994).

Roshitschek-Schimmel (1983) pointed out that seeds are of no importance for the propagation of *Urtica* but emphasized their importance for the colonization of new sites. Once the plant is established, it can rapidly develop a large and dense population by rhizome growth (see also Klimešová 1995).

Urtica seedlings usually fail to establish due to the shading from the herb layer. On pastureland, seedlings may gain some establishment success as a result of late summer germination. Seedling establishment in woodlands could only take place unless the nutrients were not limiting and shading from the surrounding vegetation was not too high (Wheeler 1981). The results of Roberts et Boddrell (1984) supported the oppinion Greig-Smith (1948) that although occasional seedlings may be found in autumn, the main bulk is produced in the spring.

Plants established from seed mostly initiate vegetative spread as early as in the first growing period. Rhizomes produced in the late summer can reach up to 2.5 m in diameter by the following year (for *U. dioica* subsp. *gracilis*; Basset et al. 1977). Large patches resulting from rhizome growth may increase by 35-45 cm per year (Greig-Smith 1948). Even faster spread may be, however, assumed in fertile sites. The broken pieces of rhizome readily re-root to form new colonies and dense stands (Bredemann 1959, Grime et al. 1989). The clones studied by Bassett et al. (1977) were at least 50 years old.

Architecture of shoots and rhizome system

Urtica dioica is a clonal rhizomatous, polycarpic perennial, with a chamaephyte life form (sometimes considered as a hemicryptophyte; Hejný et Slavík 1988). The plants form an extensive sympodial system of rhizomes and stolons. The stem (shoot) is usually erect, up to >2 m tall, and bears opposite, decussate leaves which differ in shape according to the position on the stem: the lower leaves are ovate, ± cordate, the upper ones ± lanceolate. The mean area of the leaf is <4,000 mm^2. Numerous vegetative lateral shoots (branches) growing from stipules at the base of stem leaves are often produced in late summer and autumn. Stem and leaves are more or less densely covered with hairs and stinging hairs, the latter being absent from the inflorescence. The species is dioecious, with four axillary inflorescences in each node (Olsen 1921; Greig-Smith 1948; Grime et al. 1989).

New rhizomes (reddish in colour) are mainly produced in late summer or autumn either from older rhizomes or from stem bases. These rhizomes bear stinging hairs and scale leaves with small rudimentary lamina and large stipules. Roots develop immediately above the stipules (four per node). The roots branches profusely and forms numerous laterals. Older rhizomes and roots are covered with yellow cork layer. (Greig-Smith 1948). Roots usually lack mycorrhizas (Grime et al. 1989).

Most shoots develop from new horizontal rhizomes in the autumn. They may overwinter, though some of them decay, and resume growth during the following spring. Approximately one-third of the maximum shoot biomass is maintained over the winter (Al-Mufti et al. 1977).

The allometric relations are affected by nutrient supply and fluctuation of groundwater table (Šrůtek 1995, Šrůtek, submitted).

Competitive ability

Grime et al. (1989, p. 24) designated *Urtica dioica* as a strong competitor. Schmidt (1981, 1986) investigated competitive relationships in replacement experiments with *Solidago canadensis* and *Urtica dioica*. Whereas in monocultures the growth of both species showed was increased under favourable nutrient and soil conditions, *Urtica* displaced *Solidago* completely from the mixture on the loam rich in nitrogen. *Solidago* was more successful on the nitrogen-poor sand, but even then did not outcompeted *Urtica* totally.

Winsor (1983) compared germination behaviour and seedling emergence and growth of annual *Impatiens capensis* with those of two perennials, *Urtica dioica* and *Eupatorium maculatum*, in order to find out whether or not the *Urtica* plants could establish in *Impatiens* stands. The capability of *Urtica* seedlings to survive until the end of the first growing period may permit them to become established provided that the continuity of *Impatiens* canopy is broken by lodging or trampling. However, *Urtica* grown from rhizome pieces penetrated into the *Impatiens* stand, and in a few cases overtopped its canopy.

Hara et Šrůtek (1995) found that *Urtica* exhibits negatively size-dependent shoot mortality and density-dependent shoot self-thinning from the beginning of the growing season, but competition was almost absent among living shoots. It is hypothesized that the resources of smaller shoots subjected to self-thinning are absorbed by larger living shoots, resulting in the support of growth of the latter and hence reducing the shoot competition.

Urtica is capable of suppressing the growth of other herbaceous plants which, together with the impact of relatively persistent stem litter, often leads to the species forming monospecific stands (Al-Mufti et al. 1977, Grime et al. 1989, Šrůtek 1993). The leaf dehiscence starts as early as in the summer so that there is a dense litter layer which rapidly decays on the soil surface (Schmidt 1983). The decomposition of *Urtica* matter is faster in deciduous hardwood forests than in grasslands (Zucker et Zech 1987). Smažík (1982) documented the allelopatic effects of extracts from *Urtica* aboveground biomass on germination of several ruderal species (e.g. *Matricaria maritima, Arctium tomentosum, Artemisia vulgaris*).

Debilitation of competitive ability (e.g. premature decline in shoot dry weight, reduction in flowering etc.) occurs in forest understory due to shading, and coincides with the full expansion of tree canopy (Al-Mufti et al. 1977). Competitive ability of *Urtica* may be also reduced by grasses (Bassett et al. 1977) or on infertile soils, where it was associated with a marked decrease in growth rate (Rorison 1967).

Of a few species capable of persisting in almost monospecific *Urtica* stands, a winter annual *Galium aparine* is the most successful competitor of *Urtica*. As a climber, *Galium* can maintain growth and cause physical destruction of the *Urtica* canopy by its weight resting on the host stems (Schulze et Chapin III 1987). The physical support, resembling *Urtica* stems, affects performance and mortality of *Galium*, especially at the highest density (Puntieri et Pyšek 1993).

Growth characteristics

Urtica dioica, being a plant of fertile habitats, has higher relative growth rate (2.0-2.4 week^{-1}) than species associated with infertile habitats. It belongs to the group of plants in which the high yield is associated rather with exceptionally high maximum potential relative growth rate R_{max} than with high seed weight (Grime et Hunt 1975).

The specific leaf area increases in response to shading (Wheeler 1981). On the other hand, as a shade-intolerant species, *Urtica* exhibits poor flowering and truncated shoot phenology in woodland habitats (Al-Mufti et al. 1977). Wheeler (1981) concluded that, when assessed on the basis of extension growth and leaf area ratio (LAR), seedlings show a great inter-clonal variation in their response to shading. Significant differences in extension growth were found both within and between woodland and pastureland clones.

Corré (1983a) found no differences between plants of sunny and shaded habitats in adaption of either leaf area ratio (LAR) or net productivity (NAR) to light intensity. The same holds for relative growth rate (RGR). In *Urtica*, however, he documented an adaptation of shade plants to low light intensities. Compared to *Galinsoga parviflora, Urtica* plants exhibited lower RGR under all light intensities but a very low one. This makes it possible for the species to adjust its growth by minor adaptations to the light conditions without necessity for redistribution of dry matter (Corré 1983b).

Květ (1978) gives several growth-analytical characteristics for *Urtica* and found different values in two contrasting habitats, represented by woodland and clearing (Table 1). He emphasized that individual variation among shoots appears to be due to an interference between the environmental and internal factors such as apical dominance of the terminal rhizome buds in plants of a different age.

Table 1. Growth-analytical characteristics for *Urtica dioica* (from Květ 1978). A - leaf area, Wl - dry weight of leaves, Ws - dry weight of stems + petioles, W - total shoot dry weight, LAR - leaf area ratio, SLA - specific leaf area, LWR - leaf weight ratio. Mean values are given (n = 10 for dry weight, n = 5 for leaf area). Flowering shoots were sampled.

Characteristics	A (dm^2)	Wl (g)	Ws (g)	W (g)	LAR ($dm.g^{-1}$)	SLA ($dm.g^{-1}$)	LWR (%)
Woodland	8.88	2.12	5.23	7.36	1.32	4.52	29.2
Clearing	3.71	1.97	6.39	8.31	0.47	2.05	24.6

Effects of cutting

Urtica dioica is very sensitive to regular and frequent cutting (van der Maarel 1980, Šrůtek et al. 1988). For example, the stands of tall forbs and grasses with dominant *Urtica* in abandoned former orchards developed to grassland vegetation with dominant *Arrhenatherum elatius* after the mowing was applied (van der Maarel 1984). Similarly, regular cutting proved satisfactory for reducing dominant tall vegetation with *Urtica dioica, Cirsium arvense, Arctium minus*, etc. (Worrall et Palmer 1988).

Herbivory

Living shoots of *Urtica* are rather unpalatable for livestock (Kuliev et al. 1986) because of stinging hairs covering densely the surface of above-ground parts of the plant (Thurston et Lersten 1969). Fresh and old leaves were, however, found palatable for some snails (Grime et al. 1968, Grime et Blythe 1969). *Urtica* may be grazed by animals and intense grazing may contribute to seed dispersal. Haeggström (1990) found that sheep droppings contained numerous germinable *Urtica* seeds. In addition, selective grazing by sheep and cattle favoured some species, *Urtica* among them (see also Kuliev et al. 1986).

Pollard et Briggs (1984) investigated the effects of sheep and rabbit grazing on the density of stinging hairs of *Urtica*. They concluded that both herbivores preferred plants with lower stinging hair densities. It was suggested by herbivore behaviour that stinging hairs act to deter consumption of significant amounts of plant matter. The variability in the number of stinging hairs has a genetic basis.

Pullin et Gilbert (1989) found that the grazing pressure leads to higher trichome densities in grazed compared to ungrazed areas as a results of selection for more heavily defended plants and/or because the trichome density on regenerated parts of grazed plants was increased.

Pullin (1987) tested hypothesis that the interruption of normal plant phenology may provide opportunities for insect herbivores to escape from nutritional constraints. He used *Urtica* as a test food-plant and caterpillars of a nymphalid butterfly *Aglais urticae* as its herbivore specialist. Plants subjected to cut showed increased water content and nitrogen levels in leaves compared to the control, and the herbivore exhibited improved feeding efficiency, faster development, greater weight at pupation, and possibly increased fecundity (Pullin 1986 a, b). *Aglais urticae* normally completes two generations a year, but the third generation occurred during the experiment. Pullin (1987) suggested that this extra generation was a response to increased availability of good-quality food.

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chapter 2

DISTRIBUTION OF THE STANDS WITH *URTICA DIOICA* L. ALONG THE LUŽNICE RIVER FLOODPLAIN ON THE BORDER BETWEEN AUSTRIA AND CZECHOSLOVAKIA AND LAND MANAGEMENT

Vegetatio 106: 73–87, 1993.

Distribution of the stands with *Urtica dioica* L. along the Lužnice River floodplain on the border between Austria and Czechoslovakia and land management

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Accepted 4.8.1992

Keywords: Austria, Crosswise transects, Czechoslovakia, Gradient analysis, River floodplain, Management, Species richness, *Urtica dioica*

Abstract

The effects of different management practices (mainly mowing, grazing, nutrient enrichment) on floodplain vegetation were compared between the Austrian and Czech part of the Lužnice River floodplain using nitrophilous vegetation with *Urtica dioica*. The vegetation samples situated on crosswise transects (40 in total) were used for the analysis of vegetation. Correlations between the floodplain width on these transects and the proportions (expressed as percentage of the total floodplain width) of selected characteristics (*Urtica dioica* and *Phalaris arundinacea* stands and managed areas) were not statistically significant. Differences in the proportions of selected characteristics between the two parts of the floodplain were not significant either, except differences in the proportion of 'managed areas' and 'species richness' (higher species richness and proportion of managed areas are in the Austrian part of the floodplain). The different environmental variables were used in ordinations (DCA and CCA) of vegetation samples. In the DCA, four groups of samples were interpreted. In the CCA changes the moisture gradient was the most important one. The transect distance (from the first transect in Austria) and the soil moisture had the closest relationship to the species data.

Nomenclature: follows Ehrendorfer, F. 1973. Liste der Gefässpflanzen Mitteleuropas. Gustav Fischer, Stuttgart; Holub, J., Hejný, S., Moravec. J. & Neuhäusl, R. 1967. Übersicht der höheren Vegetationseinheiten der Tschechoslowakei. Rozpr. Čs. Akad. Věd, řada matemat. přírod. věd 77: 1–76.

Introduction

Wetlands, an estimated 6% of the world land surface, belong to the most investigated and also to the most endangered world ecosystems. Three main factors are considered to be critical for wetland ecosystems: water level, nutrient status, and the natural disturbance. Modification of any of the factors, through human activity, can lead to wetland alteration, either directly or indirectly (Mitsch & Gosselink 1986).

The Třeboň Basin area provides an example of complex human impact on wetlands in Czechoslovakia. Great attention has been paid to wetland ecosystems for a long time (Dykyjová & Květ 1978; Hejný *et al.* 1986). Recently, the Lužnice River floodplain is in the focus of attention (Prach *et al.* 1990). The upper part of the floodplain is divided between Austria and Czechoslovakia, two countries differing (in the past) in their social regime. Those differences are reflected also in landscape management.

As a result, the species diversity of the floodplain vegetation decreases in the direction from Austria to Czechoslovakia (see below) and species with strong competitive ability (e.g. *Rumex obtusifolius*, *Urtica dioica* and *Phalaris arundinacea*) prevail especially in many areas of the Czech part of the floodplain. Nitrophilous vegetation with dominant *Urtica dioica* provides a good example of change of the species structure.

The present paper concerns stands of *Urtica dioica* in the floodplain along the upper part of the Lužnice River. *Phalaris arundinacea* is used as a comparative species in many cases because its stands are also very common in the Lužnice River floodplain (Fig. 1).

The paper aims at answering the following questions:

(1) Are the proportions (widths expressed as percentage of the total floodplain widths) of the managed areas (pastures, mowed meadows and fields) and the proportions of the *Urtica* and *Phalaris* stands, which were measured on the regularly placed crosswise belt transects, correlated with the total floodplain widths on those transects?
(2) Do the proportions of *Urtica* stands on the transects differ between the Austrian and the Czech part of the Lužnice River floodplain?
(3) Are there differences in species richness of *Urtica* stands between the Austrian and the Czech part of the floodplain? What invasive species are present?
(4) What are the environmental determinants of the species composition of floodplain communities?

Study area

The study area involves the Lužnice River floodplain between the Austrian village of Fischbach (14° 16′ E, 48° 38′ N) and the Rožmberk Fishpond in ČSFR (South Bohemia; 14° 01′ E, 49° 46′ N; near the town of Třeboň) e.g., from the 190th to the 96th river kilometer (Fig. 1). The landscape topography varies from upland to lowland. The altitude of the floodplain bottom varies from 656 m to 428 m a.s.l.

The geological substratum is formed mostly from granodiorite and paragneiss in the Austrian hilly part of the floodplain; the South Bohemian part of floodplain is composed of two to three Pleistocene terraces of Riss and Würm period (Chábera *et al.* 1985). The observed floodplain width varies approximately from 20 to 800 m (Table 4).

The climatic characteristics taken from two stations (Weitra, Austria, 580 m a.s.l. and Třeboň, ČSFR, 433 m a.s.l.) are: mean annual temperature 6.6 °C and 7.8 °C, and precipitation 695 mm and 627 mm, respectively (Prach *et al.* 1990).

The Austrian and the Czech parts of the floodplain differ in agricultural management. The differences in land use are also reflected in species diversity of the vegetation (Prach *et al.* 1990). The Lužnice River floodplain has been extensively used for centuries by farmers from estates scattered along the river. Small farms have been preserved only in the Austrian part of the floodplain, where the species diversity of meadows and pastures outlived owing to regular moving and absence of over-fertilization.

Great changes in meadow and wetland management have taken place during the last 30 to 40 years in the Czech part of the floodplain. Large areas in this Czech part have been changed into intensively used permanent grass stands with artificially sown grasses while the wetter parts of the floodplain have ceased to be used at all. Consequently, original wetland vegetation of the abandoned sites has changed into wet ruderal stands often with prevailing *Phalaris arundinacea* and *Urtica dioica* (both species also create poor monospecific stands). Considerable changes in species composition are also observed in the intensively manured (by piggery sewage), regularly mown meadows (2 to 3 times a year).

From the point of view of the Zürich-Montpellier classification system the investigated

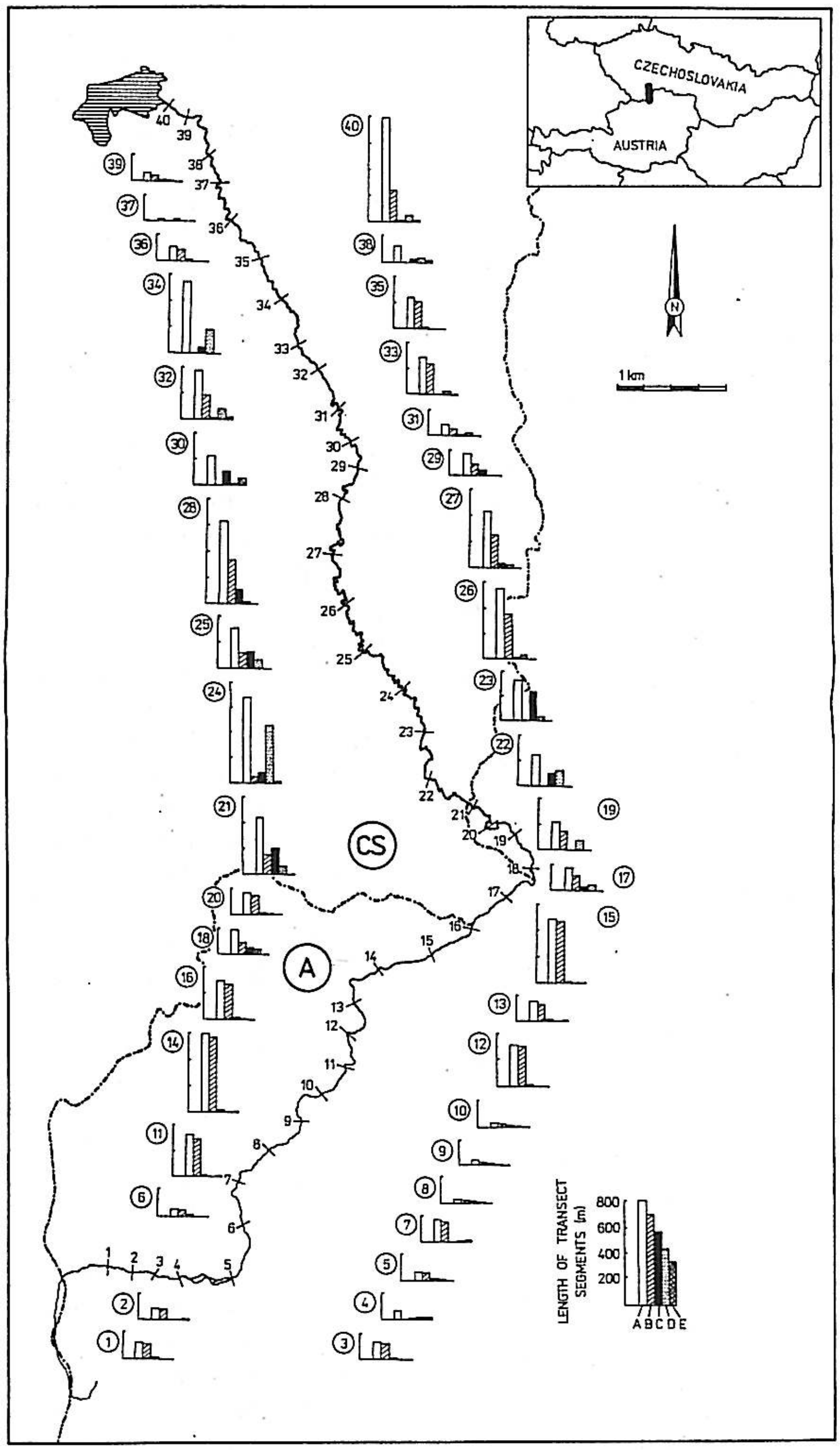

Fig. 1. Distribution off crosswise transects in the upper part of the Lužnice River floodplain in Austria (A) and Czechoslovakia (CS). Transect numbers correspond with diagram numbers 1 to 40. Description of diagram: A – floodplain width, B – width of managed and other man-affected areas (pastures, mowed meadows, fields, old fields, dumps, roads etc.), C – width of *Urtica dioica* stands, D – width of *Phalaris arundinacea* stands, E – width of stands, in which the cover of both species is in relation 1:1.

stands with *Urtica dioica* can be ranked into the following higher phytosociological units: class *Alnetea glutinosae* Br.-Bl. et Tüxen 1943 (woods with *Alnus glutinosa* along the river), class *Galio-Urticetea* Passarge ex Kopecký 1969 (unshaded stands with *Urtica dioica* in floodplain), class *Phragmiti-Magnocaricetea* Klika in Klika et Novák 1941 (unshaded stands with prevailing *Phalaris arundinacea*; Holub *et al.* 1967).

Material and methods

Vegetation samples of the same size (2 by 4 m) were taken on regularly placed belt transects (in vegetation seasons 1988 and 1989) crossing the youngest terraces of the floodplain. The transects were about 2 km apart (Fig. 1). The widths of the *Urtica* (and *Phalaris*) stands (stands with any occurrence of *Urtica* and *Phalaris* shoots) were measured. Samples were taken from the centre of all Urtica and Phalaris stands on the transects. However, if the size of a clone (*Urtica* or *Phalaris*) was smaller than the shorter side of a sample (2 m), the clone was placed in the centre of the sample. The total number of the obtained samples from the observed stands was 215 (66 in the Austrian part, 149 in the Czech part).

The species cover was estimated with 5% accuracy. For rare species the following levels of the Braun-Blanquet's scale were used: r, +, 1 (Braun-Blanquet 1964). For mathematical processing these levels were replaced by values 0.02, 0.1, and 2.5, respectively (van der Maarel 1979). The widths of stands with *Urtica dioica*, of other vegetation types (*Phalaris* stands; managed areas – mowed meadows, pastures, fields and temporarily abandoned fields; shrubs, small woods, forests etc.), of roads, ways and the whole floodplain in the position of each transect were measured by pacing followed by recalculation into metres (Table 4). These characteristics were expressed as percentage of the total floodplain width. The percentage values were subjected to the arcsine transformation (Zar 1974).

Correlations between floodplain width and proportion of some above-mentioned characteristics were evaluated by Pearson's correlation coefficient (Zar 1974; Table 4).

The differences between the Austrian and the Czech parts of floodplain (transects No. 1 to 21 and 22 to 40, respectively) were evaluated by Mann-Whitney test (Zar 1974) applied to the following characteristics: the width of managed areas, the width of all *Urtica* and *Phalaris* stands separately as well as the width of unshaded stands of those species separately. The same kind of test was used for evaluating the differences in species number in the samples (only for *Urtica* stands) between the two groups of transects.

Two types of ordination analyses were performed (DCA – detrended correspondence analysis, CCA – canonical correspondence analysis; Ter Braak 1987a, 1987b):

In the DCA the following environmental variables were used (letters correspond with those in Fig. 2):

1) Quantitative (and semi-quantitative) variables:
- the floodplain width in the position of each transect (A),
- the distance of each transect from the starting point (i.e. from the first transect in Austria, B),
- the distance of the vegetation sample from the river bank (C);
- cover of the tree, shrub and herb layers, respectively (E_1,E_2,E_3);
- cover of *Urtica dioica* (E_4);

2) Nominal variables:
- the stand character (non-managed areas in the open floodplain, river banks (0 to 10 m in width) without trees, dumps, small woods in the open floodplain, river banks with trees and/or shrubs; F_1,F_2,F_3,F_4,F_5),
- the type of agricultural management (unmoved meadows; mowed meadows; non-managed stands on the river banks with scattered trees and/or small non-managed woods; G_1,G_2,G_3).

Two first quantitative variable characterizes transects (each samples in particular transects has the same value of these variables). The rest of variables characterize samples.

In the CCA (Fig. 5), the species were charac-

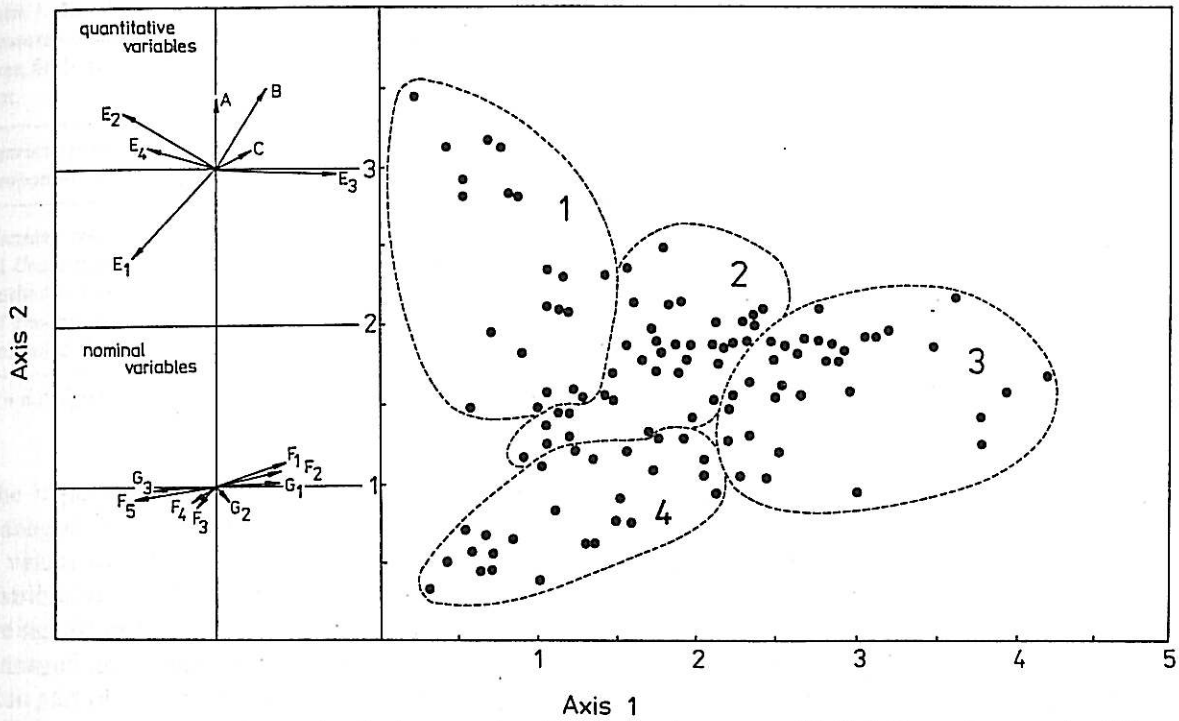

Fig. 2. DCA ordination of the samples. For interpretation of groups 1 to 4 see text and Table 3. The environmental variables are: 1) Quantitative (and semi-quantitative) variables: A – floodplain width in the position of each transect; B – distance of each transect from starting point (i.e., from the first transect in Austria, see Fig. 1); C – distance of vegetation sample from the river bank; E_1,E_2,E_3 – cover of the tree, shrub and herb layers, respectively; E_4 – cover of *Urtica dioica*; 2) Nominal variables: F_1,F_2,F_3,F_4,F_5 – stand character (non-managed areas in open floodplain; river banks (0 to 10 m in width) without trees; dumps; small woods of the open floodplain; river banks with trees and/or shrubs, respectively; G_1,G_2,G_3 – type of agricultural management (unmowed meadows; mowed meadows; non-managed stands on the river banks with scattered trees and/or small non-managed woods, respectively). The group 2 contains *Urtica* stands with highest values of cover of Urtica dioica (Table 3). Important environmental variables tend to be represented by longer arrows than less important environmental variables. The position of the 2 particular arrows (variables) to each other reflects the degree of their weighted correlation. The nearest arrows, variables, have the strongest weighted correlation.

terized by three semi-quantitative Ellenberg's species indicator values (soil moisture, soil reaction and nitrogen content in the soil; Ellenberg 1974; Persson 1981; Klimeš 1987).

The Monte Carlo permutation test was used for testing statistically whether the species composition is related to supplied environmental variables (Ter Braak 1987a).

Results

The evaluation of Urtica *dominance and of the proportion of the managed habitats in the floodplain of the Lužnice River*

The applied method of data sampling enables to correlate the parameter 'floodplain width' with other measured characteristics (see Material and methods; Table 4, Fig. 1).

When evaluating data the following hypothesis was tested: values of the selected characteristics linearly depend on floodplain width. This hypothesis can be rejected because the linear correlation was not significant in any case (see Table 1). The r-value is very closed to critical value only in the case of all *Urtica* stands in the Czech part of the floodplain.

The following hypothesis was used for evaluating differences in selected characteristics between the Austrian and the Czech part of the floodplain: values (proportions) of measured characteristics (see Material and methods) are approximately the same in both floodplain parts.

Table 1. Results of the correlation (values of Pearson's correlation coefficients) of the parameter 'floodplain width' with other measured characteristics: proportion of *Urtica* (and *Phalaris*) stands and proportion of managed areas (mowed meadows, pastures, fields and temporarily abandoned fields). Number of transects: n = 21 for the Austrian part of floodplain, n = 19 for the Czech part.

Characteristics (proportion of ...)	Total floodplain	Austrian part	Czech part	Significance level
Managed areas	– 0.143	0.201	– 0.039	ns
All *Urtica* stands	– 0.191	– 0.109	– 0.420	ns
Unshaded Urtica stands	0.132	0.351	– 0.053	ns
All *Phalaris* stands	0.204	– 0.153	0.260	ns
Unshaded *Phalaris* stands	0.267	– 0.020	0.283	ns

ns = not significant, $P < 0.05$.

The hypothesis was rejected in the case of the managed areas and species richness because the U values were lower than the critical values of U distribution (Tables 2 and 4). It means that there are significantly higher proportions (values) of the managed areas and species richness in the Austrian part of the floodplain than in the Czech part.

The species-richest stands with *Urtica* were found in the Austrian part of the floodplain in the area with regularly mowed meadows. A lot of species from these rich meadows have been found even in river bank stands with *Urtica* and *Phalaris*.

The occurrence of some invasive species spreading along the river is interesting: *Epilobium adenocaulon*, *Impatiens glandulifera*, *Rudbekia laciniata*, and *Spiraea salicifolia*.

Ordinations

DCA ordination

In the DCA ordination (Fig. 2) eigenvalues of the first four axes ($l_1 ... l_4$) were 0.56, 0.50, 0.39 and 0.33, respectively. Values over 0.5 often denote a good separation of the species along the axis. As l_3 and l_4 are small compared to l_1 and l_2, the third and the fourth ordination axes can be ignored and the first two ordination axes can be expected to display the biologically relevant information (Jongman *et al.* 1987).

Identifiable groups of samples are not strictly separated in the ordination space (Fig. 2; important environmental variables tend to be repre-

Table 2. Results of the Mann–Whitney test (U values for Austrian and Czech part of floodplain) evaluating differences in selected characteristics between the Austrian and Czech part of the floodplain. Number of transects: n = 21 for the Austrian part of floodplain, n = 19 for the Czech part. Number of samples (only from *Urtica* stands) for species richness evaluation: n = 55 for the Austrian part, n = 111 for the Czech part. The basic characteristics of species richness are: for the Austrian part, range of species number is 2 to 23 (mean 8.2, standard deviation 5.5, coefficient of variance 67.1); for the Czech part, 1 to 19 (mean 5.1, SD 3.2, coef. var. 62.7); for the whole observed floodplain, 1 to 23 (mean 6.1, SD 4.3, coef. var. 70.5).

Characteristics (proportions of ...)	Austrian part	Czech part	Significance level
Managed area (see Table 1)	76	340	*
All *Urtica* stands	270	130	ns
Unshaded *Urtica* stands	299	282	ns
All *Phalaris* stands	276	155	ns
Unshaded *Phalaris* stands	297	186	ns
Species richness	103	74	**

ns = not significant, * $P < 0.05$, ** $P < 0.01$.

sented by longer arrows than less important environmental variables, Ter Braak 1986; the position of the particular arrows, variables, to each other shows their weighted correlation; the nearest arrows, variables, have the strongest weighted correlation). This indicates a transition between different types of *Urtica* stands from the point of view of species composition. Spatial and species heterogeneity of *Urtica* stands is large: it ranges from stands with different degree of tree and shrub shading to completely open areas, from rare occurrence of *Urtica* to stands dominated by this species, from weeded forest edges to natural vegetation of river banks with shrubs and trees, from irregularly mowed meadows to entirely non-managed areas etc.

The interpretation of groups can be roughly completed in the following way (Fig. 2, Table 3): a) group 1 represents riparian stands of willows (and poplars) in the tree and/or shrub layer and groups of shrubby willows in the open floodplain (*S. fragilis* is dominant in the tree layer, *S. cinerea* is in the shrub layer); *Glechoma hederacea*, *Aegopodium podagraria*, *Galium aparine* and *Lamium maculatum* are the most frequent species in the herb layer; b) group 2 represents non-managed open floodplain and/or river bank stands with rare occurrence of trees and shrubs (*Salix fragilis* is the most frequent); *Galium aparine*, *Symphytum officinale*, *Angelica sylvestris* and *Filipendula ulmaria* are the most frequent species; c) group 3 contains samples of the similar habitats as group 2 (*Alnus glutinosa* and *Salix fragilis* dominate the tree and the shrub layer, respectively); a high dominance of *Phalaris* is common in the herb layer (a higher species richness is evident in these stands); *Galium aparine*, *Symphytum officinale*, *Filipendula ulmaria*, *Galeopsis pubescens* and *Carex brizoides* are frequent; d) group 4 represents mostly stands of frequently disturbed small woods with a high species richness and species-rich *Urtica* stands of the river bank of the Austrian part of the floodplain (in comparison with previous groups); stands on the margins of waste places and on the drier bases of terraces occur in this group too; the cover of *Urtica* and *Phalaris* is low; *Aegopodium podagraria*, *Lamium maculatum* and *Carex brizoides* are the most frequent species; the meadow species are more common in herb layer of the Austrian stands (e.g. *Trisetum flavescens*, *Stellaria media*, *Linaria vulgaris*, *Alopecurus pratensis*, *Ranunculus acer*).

The abundance or probability of occurrence of a species tends to decrease with its distance from the centre of the diagram (Fig. 3; compare Ter Braak 1986; Ter Braak & Prentice 1988). Species near the centre of the diagram are frequently ubiquitous (e.g. *Urtica dioica*, *Symphytum officinale*, *Filipendula ulmaria*, *Cirsium oleraceum*, *Ranunculus repens*, *Aegopodium podagraria*, *Stellaria nemorum*, *Dactylis glomerata*, *Phalaris arundinacea*, *Lamium maculatum*) in our data sets. The species points on the edge of the ordination diagram are often rare species in the data sets (e.g. *Calama-*

Table 3. The main characteristics of 4 distinguished groups of vegetation samples in DCA ordination space (Fig. 2).

Main characteristics	Group number			
	1	2	3	4
mean cover of layers and species/ range of values (%)				
– tree layer	25/0–70	1.5/0–20	2.5/0–40	30/0–75
– shrub layer	30/0–70	2/0–30	0.5/0–15	13/0–70
– herb layer	60/25–90	90/70–100	95/50–100	70/30–100
– *Urtica*	40/10–90	70/5–95	10/1–40	30/5–60
– *Phalaris*	10/0–40	15/0–65	70/0–100	9/1–40
Average species richness/ range of values	7.4/3–17	5.5/2–13	6.7/2–19	10.9/3–23

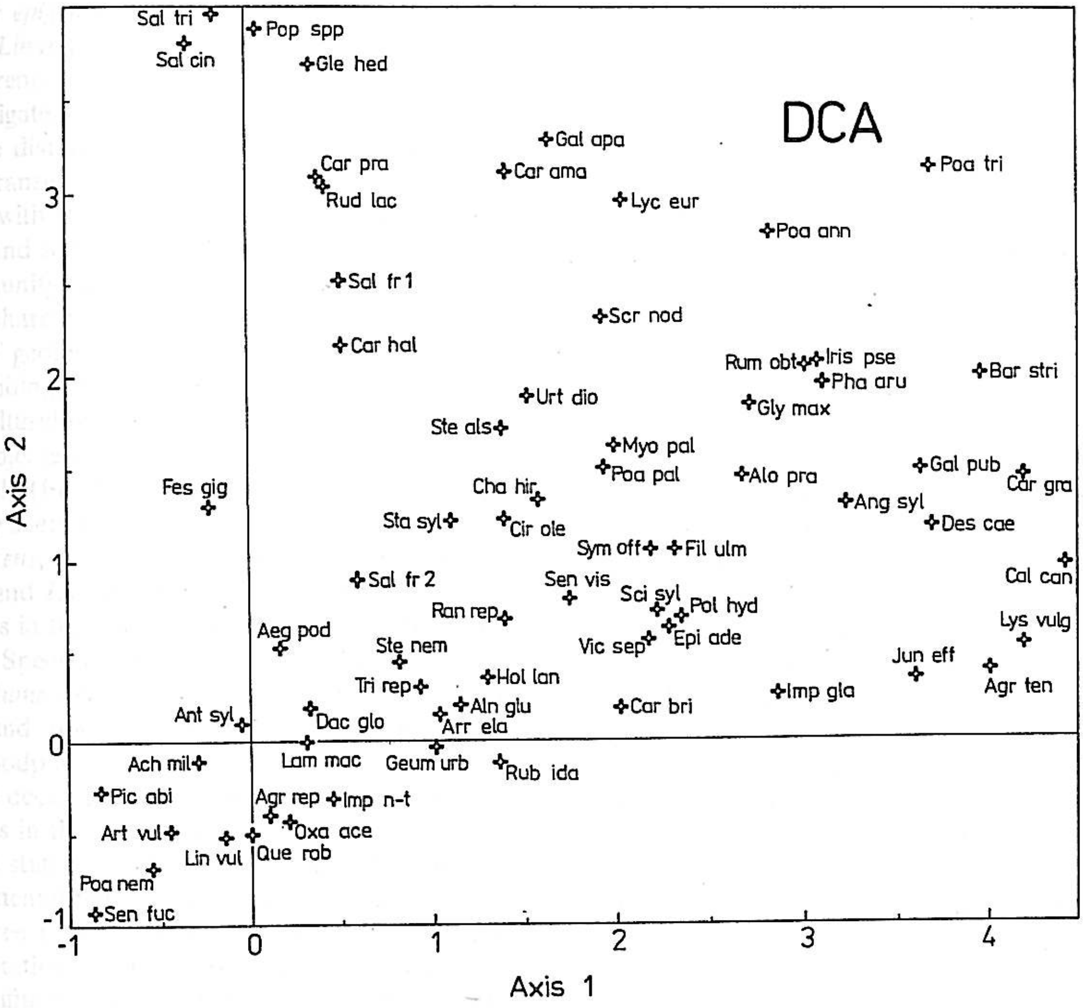

Fig. 3. DCA diagram of species. Ach mil = *Achillea millefolium*, Aeg pod = *Aegopodium podagraria*, Agr rep – *Agropyron repens*, Agr ten = *Agrostis tenuis*, Aln glu – *Alnus glutinosa* (tree), Alo pra = *Alopecurus pratensis*, Ang syl = *Angelica sylvestris*, Arr ela = *Arrhenatherum elatius*, Art vul = *Artemisia vulgaris*, Ant syl = *Anthriscus sylvestris*, Bar str = *Barbarea stricta*, Cal can = *Calamagrostis canescens*, Car ama = *Cardamine amara*, Car pra = *Cardamine pratensis*, Car hal = *Cardaminopsis halleri*, Car bri = *Carex brizoides*, Car gra = *Carex gracilis*, Cha hir = *Chaerophyllum hirsutum*, Cir ole = *Cirsium olearceum*, Dac glo = *Dactylis glomerata*, Des cae = *Deschampsia caespitosa*, Epi ade = *Epilobium adenocaulon*, Fes gig = *Festuca gigantea*, Fil ulm = *Filipendula ulmaria*, Gal pub = *Galeopsis pubescens*, Gal apa = *Galium aparine*, Geum urb = *Geum urbanum*, Gle hed = *Glechoma hederacea*, Gly max = *Glyceria maxima*, Hol lan = *Holcus lanatus*, Iris pse = *Iris pseudacorus*, Imp gla = *Impatiens glandulifera*, Imp n-t = *Impatiens noli-tangere*, Jun eff = *Juncus effusus*, Lam mac = *Lamium maculatum*, Lin vul = *Linaria vulgaris*, Lyc eur = *Lycopus europaeus*, Lys vul = *Lysimachia vulgaris*, Myo pal = *Myosotis palustris* agg., Oxa ace = *Oxalis acetosella*, Pha aru = *Phalaris arundinacea*, Pic abi = *Picea abies* (tree), Poa ann = *Poa annua*, Poa nem = *Poa nemoralis*, Poa pal = *Poa palustris*, Poa tri = *Poa trivialis*, Pol hyd = *Polygonum hydropiper*, Pop spp = *Populus* sp., Que rob = *Quercus robur* (tree), Ran rep = *Ranunculus repens*, Rub ida = *Rubus idaeus*, Rud lac = *Rudbekia laciniata*, Rum obt = *Rumex obtusifolius*, Sal fri = *Salix fragilis* (tree), Sal fr2 = *Salix fragilis* (schrub), Sal cin = *Salix cinerea* (shrub), Sal tri = *Salix triandra* (shrub),Sci syl = *Scirpus sylvaticus*, Scr nod = *Scrophularia nodosa*, Sen fuc = *Senecio fuchsii*, Sen vis = *Senecio viscosus*, Sta syl = *Stachys sylvatica*, Ste als = *Stellaria alsine*, Ste nem = *Stellaria nemorum*, Tri rep = *Trifolium repens*, Urt dio = *Urtica dioica*, Vic sep = *Vicia sepium*.

grostis epigeios, Selinum carvifolia, Oxalis acetosella, Linaria vulgaris, Senecio fuchsii). Optima of occurrence of these rare species are usually out of investigated coenoses.

The distance of particular transects from the first transect (see Fig. 1) is more closely correlated with the ordination axes than other variables, and so more closely related to the pattern of community variation (compare Ter Braak 1987b). This characteristic represents the complex gradient of geological substratum, altitude and geomorphology in the floodplain and the gradient of agricultural management. The species points can be projected on the axis of this environmental variable (Fig. 2, 3). For example *Senecio fuchsii, Oxalis acetosella, Impatiens noli-tangere, Trisetum flavescens, Leucanthemum vulgare, Prunella vulgaris* and *Lamium maculatum* are more frequent species in the narrow Austrian part of the floodplain. Species as *Urtica dioica, Phalaris arundinacea, Rumex obtusifolius* and *Barbarea stricta* can be found more often in the wider Czech part of the floodplain.

The occurrence and dominance of the selected species in the samples are shown in Fig. 4.

The statistical significance of the effects of environmental variables (except the cover of shrub and tree layers) was tested by a Monte Carlo permutation test (99 unrestricted permutations). The influence of 'the agricultural management' was not significant (P = 0.12); the influence of other variables was significant (P = 0.02).

Selected environmental variables explain a fair amount of variability in the data set. The variable 'transect distance from the first transect' has the strongest relation to the species data.

CCA ordination

Ellenberg's indicator values were used as environmental variables (Ellenberg 1979) in this case.

No evident groups of samples can be recognized in the ordination space (Fig. 5). Changing character of *Urtica* stands along the moisture gradient is the most evident, and also a well interpretable result. The abundance and dominance of *Urtica* decrease with increasing moisture. The distribution of *Phalaris* on this gradient changes in the opposite direction. This means that different types of stands with a medium to high cover of Urtica (30–100%; river bank stands with trees and shrubs, stands of the open floodplain without trees and shrubs etc.) are in the lower right quadrant of the ordination diagram. Areas with a higher soil moisture (with a higher cover a *Phalaris*, 20–100%) are in the upper left quadrant (Fig. 5).

The gradient of soil nitrogen is less evident. Its direction approximately corresponds to the second ordination axis (Fig. 5). The occurrence of nitrophilous *Urtica* is again a sufficient criterion. The samples in the upper half of the diagram have a lower cover of *Urtica* (<5 to 65%) than have samples in the lower half (as much as 100%). However, changes in the *Urtica* cover are not continuous in the direction of axis 2.

On the other hand, the gradient of soil moisture is well documented also by the exchange of further species with different demands to soil moisture (Fig. 6).

Ellenberg's indicator values were also subjected to the Monte Carlo permutation test (99 unrestricted permutations), leading, in this case, to a P-value 0.01 for all three variables. Soil moisture explains the greatest part of the variability, soil reaction the smallest one.

Discussion

Urtica dioica is a plant of open habitats and moderately shaded woodland areas (Wheeler 1981; Reif *et al.* 1985). In the Třeboň Basin its occurrence was probably restricted to river banks in the past. The first occurrence of *Urtica dioica* of anthropogenous origin was noted in the subrecent (Jankovská 1983). However, the greatest human colonization of the Třeboň Basin did not start until the 12th century. The Austrian section of the Lužnice River floodplain has been strongly modified by human impact since about 1000 A.D. (Ricek 1982).

The man-induced spreading of *Urtica dioica* is common in Central Europe at present (Ellenberg

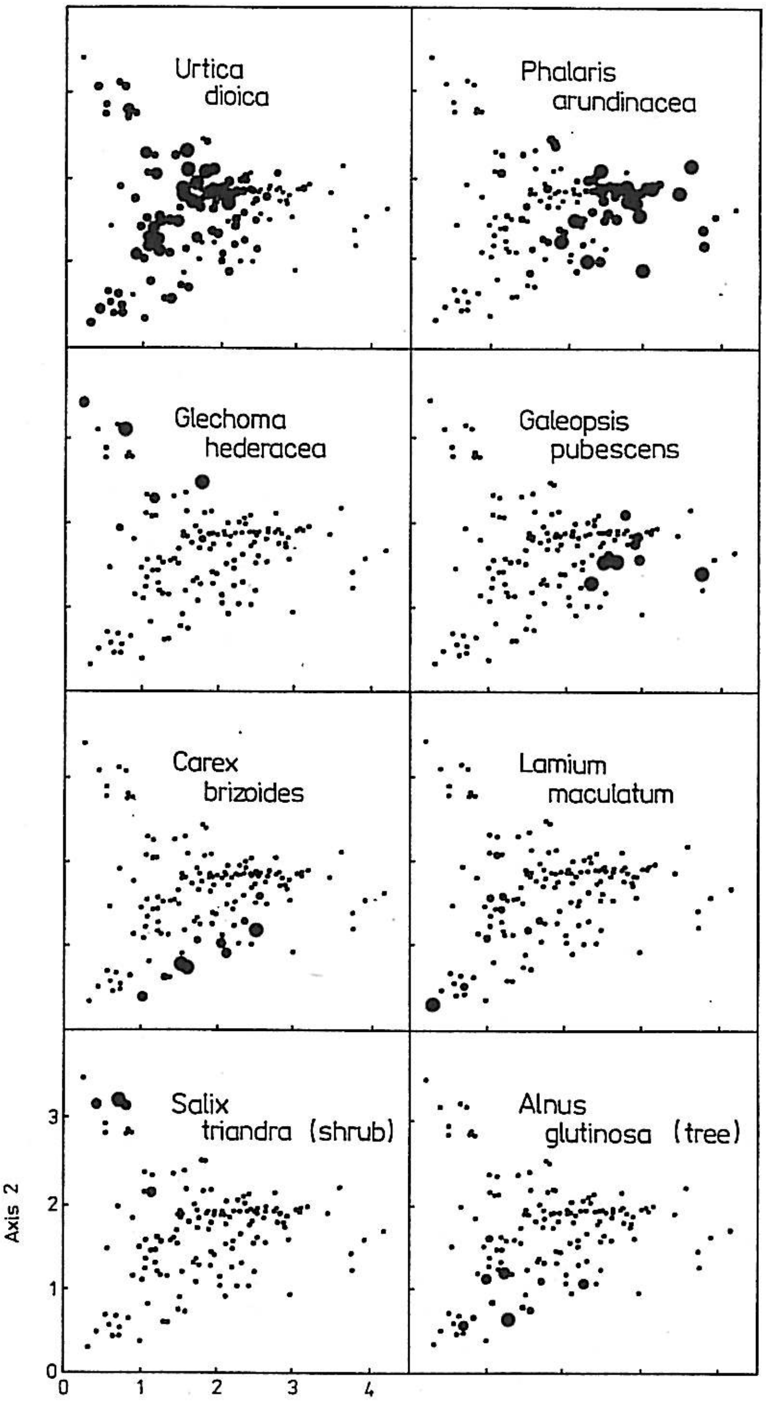

Fig. 4. Values of dominance (cover) of selected species in the DCA ordination diagram of samples (see Fig. 2). The point size represents the following ranges of cover values for the particular species: *Urtica dioica* 0.02–100%, *Phalaris arundinacea* 0–100, *Glechoma hederacea* 0–20, *Galeopsis pubescens* 0–5, *Carex brizoides* 0–60, *Lamium maculatum* 0–40, *Salix triandra* (shrub) 0–60, *Alnus glutinosa* (tree) 0–70.

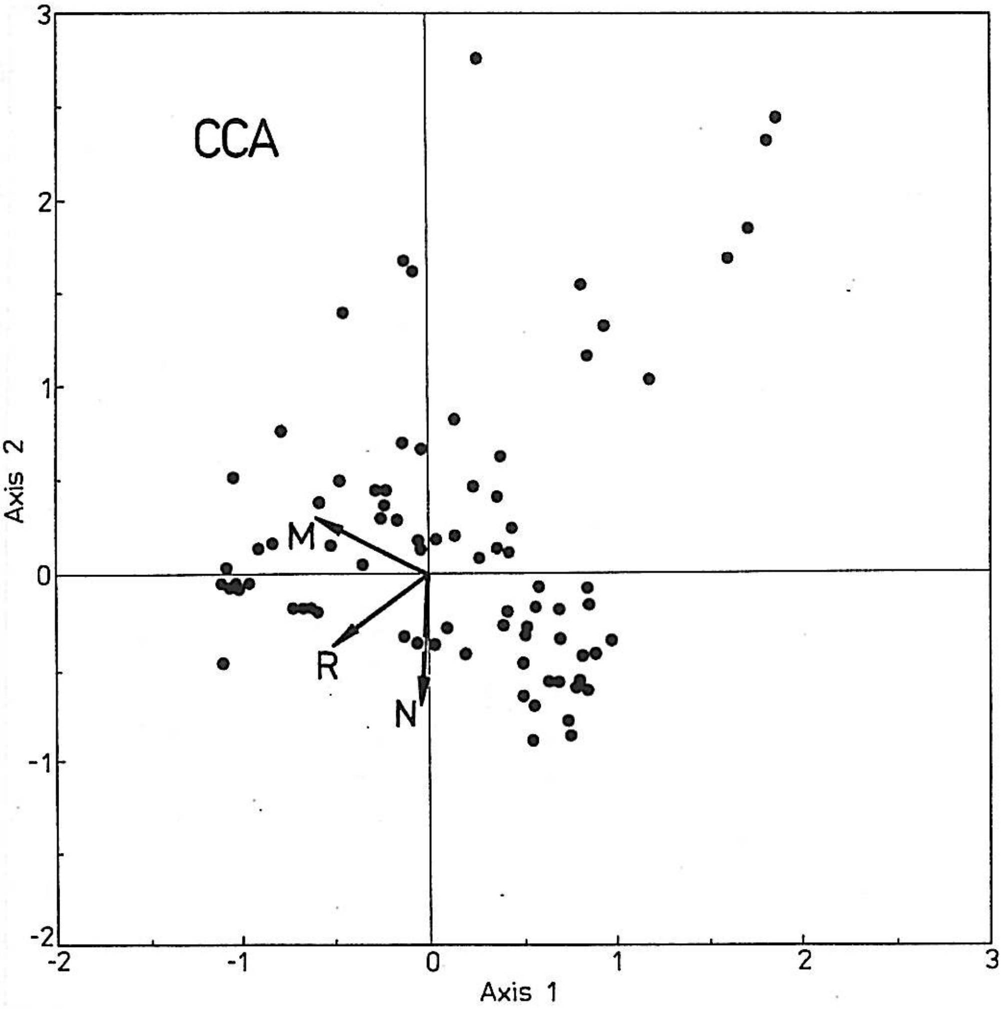

Fig. 5. CCA ordination of samples. The environmental variables are: M – soil moisture, N – nitrogen content in soil, R – soil reaction (pH).

1988). It is mainly concentrated in ruderal sites (e.g. rubbish heaps, construction sites, areas around mountain cottages, along roads etc.) and in river floodplains. The expansion of *Urtica dioica* is most progressive particularly along rivers and streams and/or in other types of wetlands (Hlaváček & Pyšek 1988; Šrůtek *et al.* 1988; Prach *et al.* 1990).

Many of the autecological features of *Urtica dioica* support the rapid spreading of this species (Grime *et al.* 1988; Wheeler 1981). On the other hand, it is very sensitive to regular and frequent cutting, which affects it considerably (van der Maarel 1980).

The answers to the introductory questions are the following:

(1) The correlations between the floodplain width and the selected quantitative characteristics (proportions *Urtica* and *Phalaris* stands and managed areas in crosswise transects) were not statistically significant in either floodplain part (the Austrian and the Czech one), nor they were along the whole observed part of the floodplain (Table 1).

(2) The comparison between the Austrian and the Czech parts of the Lužnice River floodplain of the Waldviertel and the Třeboň Basin areas was useful for the evaluation of proportions of

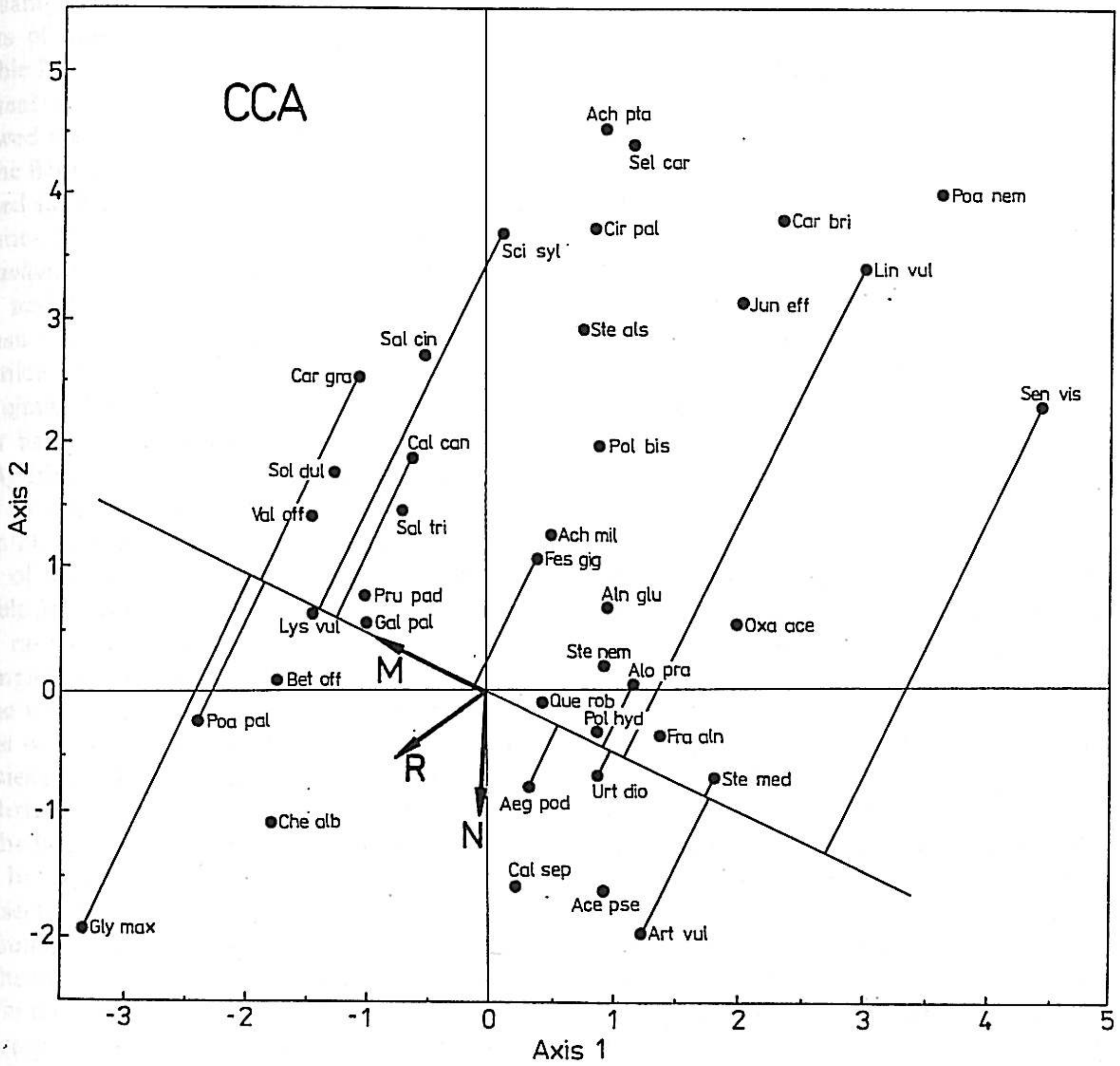

Fig. 6. CCA ordination of species. Ace pse = Acer pseudoplatanus (tree), Ach mill = *Achillea millefolium*, Ach pta = *Achillea ptarmica* Aeg pod = *Aegopodium podagraria*, Aln glu = *Alnus glutinosa* (tree), Alo pra = *Alopecurus pratensis*, Art vul = *Artemisia vulgaris*, Bet off = *Betonica officinalis*, Cal can = *Calamagrostis canescens*, Cal sep = *Calystegia sepium*, Car bri = *Carex brizoides*, Car gra = *Carex gracilis*, Che alb = *Chenopodium album* s.l., Cir Pal = *Cirsium palustre*, Fes gig = *Festuca gigantea*, Fra aln = *Frangula alnus*, Gal pal = *Galium palustre*, Gly max = *Glyceria maxima*, Jun eff = *Juncus effusus*, Lin vul = *Linaria vulgaris*, Lys vul = *Lysimachia vulgaris*, Oxa ace = *Oxalis acetosella*, Poa nem = *Poa nemoralis*, Poa pal = *Poa palustris*, Pol bis = *Polygonum bistorta*, Pol hyd = *Polygonum hydropiper*, Pru pad = *Prunus padus* (shrub), Que rob = *Quercus robur*, Sal cin = *Salix cinerea* (tree), Sal tri = *Salix triandra* (shrub), Sci syl = *Scirpus sylvaticus*, Sal car = *Selinum carvifolia*, Sen vis = *Senecio viscosus*, Sol dul = *Solanum dulcamara*, Ste als = *Stellaria alsine*, Ste med = *Stellaria media*, Ste nem = *Stellaria nemorum*, Urt dio = *Urtica dioica*, Val off = *Valeriana officinalis*. The environmental variables are: M – soil moisture, N – nitrogen content in soil, R – soil reaction. Inferred ranking (sensu Ter Braak 1987b) of the selected species along the moisture gradient is designed.

Urtica stands (and other selected characteristics) in crosswise transects (Table 2, 4; Fig. 1). However, differences in the distribution of *Urtica* stands between two parts of floodplain were not confirmed statistically. Significant differences were found only in the characteristic of the 'managed areas'.

(3) The differences in the number of species (in

the samples) between the Austrian and the Czech parts of floodplain were statistically significant (Table 2). The higher number of species was present in the *Urtica* stands on the margins of mowed meadows in the narrower Austrian part of the floodplain. Bobbink *et al.* (1987, 1988) obtained similar results in connection with different regimes of cutting and manuring. *Epilobium adenocaulon*, *Impatiens glandulifera*, *Rudbekia laciniata*, and *Spiraea salicifolia* are invasive species (sensu Bazzaz 1986), also spreading along the Lužnice River.

Rejmánek (1989) says in this connection that river banks are very rich in invasive species.

(4) Identifiable clusters of samples were difficult to separate in the DCA ordination space (Fig. 2). In spite of this fact, a rough interpretation of four groups of samples was carried out (Table 3). It is possible to separate the ubiquitous and rare species in the DCA biplot of species (compare Ter Braak 1986). The relationships of some species to the selected environmental variables was evident (e.g. a decreasing of the some species along Lužnice River from the spring area to Rožmberk fish pond, Figs. 1 and 3).

The large portion of variability in the data set can be explained by 'the distance of particular transects from the first transect' (i.e., from the beginning in Austria; Fig. 1).

The moisture gradient was the most important one in the case of the CCA ordination (Fig. 5 and 6; compare Persson 1981). The changes in dominance of *Urtica* and *Phalaris* characterize appropriately this gradient. The results of ordination confirm that *Urtica dioica* prefers moist, nitrogen-rich soils (Reif *et al.* 1985; Hempeling *et al.* 1988; Teckelmann 1987 etc.).

The largest portion of variability in the data set can be explained by 'moisture' and the smallest one by 'reaction'.

Prediction of the dynamics of the stands with Urtica dioica

The growth, development and distribution of *Urtica* stands are mainly dependent on a high nutrient availibility, on the ground water table, and on land management practices (Teckelmann 1987; van der Maarel 1980; Grime *et al.* 1988; Šrůtek *et al.* 1988; Prach *et al.* 1990). However, the management regime plays the dominant role in this respect. In our case, this is well documented by the vegetation of the Austrian part of the river floodplain, mainly of the spring area of the river, where meadows are regularly mowed. The occurrence of *Urtica dioica* is limited only to the river bank (Fig. 1). These places have the species-richest Urtica stands (see Table 3, group 4).

Urtica is a dominant species in the abandoned non-mowed open parts of the floodplain (Table 4, e.g. transect 21).

Urtica patches or clones occupy especially the elevated places or shallow depressions. *Phalaris arundinacea*, *Carex gracilis*, *Glyceria maxima* are dominant species in the deeper and moister depressions. On the other hand, *Urtica* seedlings are apparently not so closely influenced by the position of ground water table and by the type of management (Šrůtek *et al.* 1988). Moreover, the high seed production (Bassett *et al.* 1977) and the seed spreading by regular floods enable this species to occupy the most of places in the abandoned non-managed parts of the floodplain.

It is seems that the natural secondary succession leads to the dominance of *Urtica dioica* in many places of the floodplain. The water table of these places does usually not stay above the soil surface for long periods of time.

Shrubs and trees (mainly various species of *Salix*, and *Alnus glutinosa*) can expand on non-mowed sites, but their establishment is often retarded by a dense cover of the highly competitive and productive herbaceous species such as *Urtica dioica* and *Phalaris arundinacea* (Dykyjová & Květ 1978). The less robust and the less competitive grasses and herbaceous species are excluded by the strong plant competitors. Greater disturbance of the dense *Urtica* or *Phalaris* stands (e.g. by flood water) is a prerequisite for a permanent establishment of shrubs and trees and a continuation of succession.

Table 4. The basic characteristics of obtained data on the crosswise transects Nos. 1 to 40. Symbols: A – floodplain width, B – managed areas (pastures, mowed meadows, fields), C – all *Urtica dioica* stands, D – all *Phalaris arundinacea* stands; a – width (m), b – proportion (%). The transect numbers among *Urtica* and among *Phalaris* stands.

Transect number	Austrian part of floodplain							Transect number	Czech part of floodplain						
	A	B		C		D			A	B		C		D	
	(m)	a	b	a	b	a	b		(m)	a	b	a	b	a	b
1	123.0	118.0	95.9	5.0	4.1	0.0	0.0	22	239.0	0.0	0.0	99.0	41.4	119.0	49.8
2	82.0	77.0	93.9	5.0	6.1	5.0	6.1	23	328.0	0.0	0.0	236.0	72.0	32.0	9.8
3	134.0	130.0	97.0	2.0	1.5	0.0	0.0	24	673.5	50.0	7.4	85.0	12.6	447.0	66.4
4	60.0	0.0	0.0	9.0	15.0	11.0	18.3	25	317.0	97.0	30.6	132.0	41.6	74.0	23.3
5	62.0	57.0	91.9	3.0	4.8	2.0	3.2	26	550.0	351.0	63.8	11.0	2.0	35.0	6.4
6	50.0	45.0	90.0	5.0	14.0	0.0	0.0	27	426.0	246.0	57.7	35.0	8.2	23.0	5.4
7	166.0	156.0	94.0	4.0	2.4	6.0	3.6	28	626.0	338.0	54.0	109.5	17.5	13.0	2.1
8	28.0	23.0	82.1	3.0	10.7	2.0	7.1	29	172.0	87.0	50.6	41.0	23.8	0.0	0.0
9	33.5	18.0	53.7	5.0	14.9	2.0	6.0	30	224.0	0.0	0.0	153.0	68.3	54.0	24.1
10	31.5	23.0	73.0	5.0	15.9	2.0	6.3	31	85.0	53.0	62.4	4.0	4.7	20.0	23.5
11	318.5	249.0	90.7	13.0	4.1	8.0	2.5	32	374.0	181.0	48.4	24.0	6.4	102.0	27.3
12	311.0	302.0	97.1	9.0	2.9	0.0	0.0	33	283.0	235.0	83.0	0.0	0.0	30.0	10.6
13	146.0	124.0	84.9	11.0	7.5	2.0	1.4	34	544.0	0.0	0.0	54.0	9.9	186.0	34.2
14	592.0	564.0	95.3	18.0	3.0	0.0	0.0	35	240.0	211.0	87.9	14.0	5.8	0.0	0.0
15	492.5	469.5	95.3	13.0	2.6	11.0	2.2	36	114.0	90.0	78.9	17.0	14.9	0.0	0.0
16	291.0	266.5	91.6	14.0	4.8	8.5	2.9	37	16.0	0.0	0.0	16.0	100.0	0.0	0.0
17	168.0	105.0	62.5	22.0	13.1	41.0	24.4	38	123.0	0.0	0.0	42.0	34.1	50.5	41.1
18	180.0	87.0	48.3	43.0	23.9	42.0	23.3	39	61.0	49.0	80.3	5.0	8.2	2.0	3.3
19	218.0	142.0	65.1	2.0	0.9	75.0	34.4	40	792.0	248.0	31.3	7.0	0.9	57.0	7.2
20	164.0	142.0	86.6	9.0	5.5	5.0	3.1								
21	437.0	150.0	34.3	198.0	45.3	58.0	13.3								

Acknowledgements

I would like to thank Dr. G. Schlott (Ecological Station of Waldviertel, Gebharts, Austria) for his assistance during my investigations in Austria, Dr. P. Šmilauer for data processing, Dr. J. Š. Lepš for critically reading the manuscript and Miss L. Klečková for the drawings.

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chapter 3

GROWTH RESPONSES OF *URTICA DIOICA* L. TO NUTRIENT SUPPLY

Growth responses of *Urtica dioica* L. to nutrient supply

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Canadian Journal of Botany, in press

Abstract

1. This study examines the effects of nutrient supply (three N,P,K treatments: 75, 225 and 375 kg.ha^{-1}; 12.5 % N, 8.5 % P, 16 % K) on growth, allometry and architecture of *Urtica dioica* L., an expansive clonal plant found throughout Central Europe.

2. Biomass allocation was significantly affected by nutrient supply: higher nutrient doses resulted in less biomass allocation to below-ground organs while the period of intensive production of above-ground biomass was prolonged.

3. Shoot height increases with nutrient supply. The height ratios were constant over time. Within each treatment and each harvest, inflorescence biomass was positively correlated with shoot height. Branching of the main shoots (number of lateral branches) was positively correlated with plant height and changed with time. The number of new rhizomes was affected by both treatment and harvest, especially in older plants.

4. The results suggest that high nutrient supply increased the allocation of biomass both to reproductive organs and to vegetative organs.

Key-words: allometry, biomass allocation, clonal plant, nutrients, plant architecture, *Urtica dioica*.

Introduction

Clonal growth of plants and animals has been intensively investigated in the last ten years (i.e. Jackson *et al.* 1985; Harper *et al.* 1986; van Groenendael and de Kroon 1990; Callaghan *et al.* 1992). However, despite the fact that 69 out of 163 families of vascular plants include species able to proliferate vegetatively (Tiffney and Nicklas 1985) only a few species (e.g. *Trifolium repens, Solidago altissima, Ranunculus repens* and *Glechoma hederacea)* have become the subject of intensive investigation of clonal growth (Hutchings and Bradbury 1986).

Urtica dioica L. has been the object of plant population and ecological studies (see references in Grime *et al.* 1989). Physiological aspects of nutrient economy and allocation in relation to soil nutrient content have been also investigated (Pigott and Taylor 1964; Rorison 1968; Holter 1979; Hofstra *et al.* 1985; Rosnitschek-Schimmel 1985; Teckelmann 1987; Gebauer *et al.* 1988), but the reproductive effort of this plant in relation to nutrient supply has been largely neglected (Pollard and Briggs 1982; Teckelmann 1987). The term of reproductive effort used in this paper follows the article of Reekie and Bazzaz (1987a).

Urtica dioica is a widely distributed and frequently dominant species in Central Europe (Ellenberg 1986). It is expansive especially on waste-disposal- and unmanaged sites with a high supply of nitrogen and phosphorus (Pigott and Taylor 1964; Reif *et al.* 1985; Prach *et al.* 1990; Bobbink *et al.* 1992; Šrůtek 1993). Factors affecting the spreading of this species, the relation to different nutrient supply and life strategy (e.g. cost of seed production versus rhizome production) are important questions.

This paper examines the effect of different levels of nutrient supply on the production and patterns of biomass allocation within *Urtica* plants during the first growing season after germination. The following questions were addressed:

(1) What is the influence of various levels of nutrient supply on biomass allocation within the plants?

(2) What are the consequences of nutrient supply on plant architecture and allometry of various organs?

(3) Are there any changes in the ratio of cost of seed production versus rhizome production at various levels of nutrient supply?

Material and methods

Architecture of shoots and rhizome system

Urtica dioica L. (stinging nettle) is a clonal rhizomatous tall herb (height to 2 m and higher)

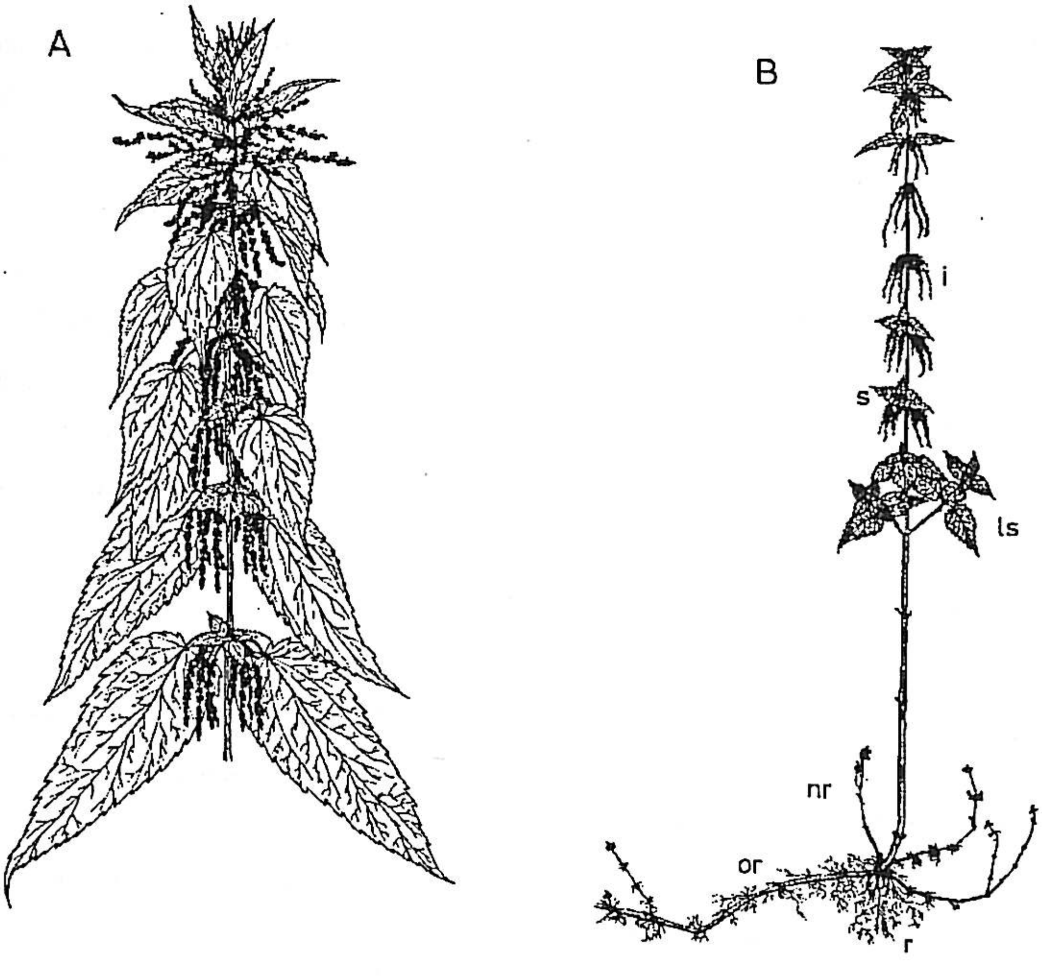

Fig. 1. Two different phenological phases of the shoot of *Urtica dioica* shoot (A - late spring, B - late autumn): i - inflorescence (infrutescence); s - stipule; ls - lateral shoot (branch); or - old rhizome; nr - new rhizome; r - roots (after Greig-Smith 1948 and Hejný & Slavík 1988, modified).

with an extensive sympodial system of rhizomes and stolons. The stem (shoot) is usually erect with opposite and decussate pairs of leaves, the lower ovate more or less cordate, the uppermore or less lanceolate. In late summer and in autumn there often takes place an abundant formation of vegetative lateral shoots (branches) which grow from stipules in the bases of stem leaves (Fig. 1). The species is a dioecious plant with axillary inflorescences, four per node.

New rhizomes (reddish in color) are mainly produced in late summer or autumn either from older rhizomes or from the stem bases. These rhizomes bear scale leaves with a small rudimentary lamina and large stipules. Roots develop immediately above the stipules (four per node). The roots branch and form numerous laterals. Older rhizomes and roots have a yellow cork layer. Vegetative spread occurs via rhizomes.

Most shoots develop from new horizontal rhizomes in the autumn. They may overwinter (some of them decay) and resume growth during the following spring.

The stems (shoots), leaves and new rhizomes are more or less densely covered with hairs and stinging hairs.

The short information presented has been extracted from various references (Olsen 1921; Greig-Smith 1948; Grime *et al.* 1989).

Experimental design

Seeds of *Urtica* from unmanaged floodplain meadows were used to set up a greenhouse experiment. The meadows are situated in the Lužnice River floodplain near the border with Austria, in the Třeboň Biosphere Reserve, South Bohemia, Czech Republic (Prach *et al.* 1990; Šrůtek 1993).

Urtica plants were grown from seeds in PVC pots (size 20 by 20 by 20 cm; 70 pots per treatment for all harvests; 210 for the whole experiment) in a plastic greenhouse without artificial air-conditioning. Consequently, the light and temperature regimes roughly follow the outside conditions (it is the natural regime in the area). Three treatments with a combined NPK fertilizer (12.5 % N, 8.5 % P, 16 % K) were compared: (1) 75 kg.ha^{-1}, (2) 225 kg.ha^{-1}, (3) 375 kg.ha^{-1}. The fertilizer was applied in aqueous solution before sowing and repeatedly after each harvest to all remaining pots. Pots were watered two times a day to achieve a constant soil moisture. During the growing season samples were taken at approximately monthly intervals starting from June 6 - six weeks after sowing - to December 5, 1990 (June 6th, July 9th, August 6th, September 8th, October 10th, November 5th, December 5th). Ten plants per treatment and harvest (except for the first harvest, where numerous seedlings - more than ten - per pot) were taken at random. From the pots remaining after the first harvest, all seedlings except the tallest one in each pot were removed.

During the experiment the following were measured: shoot height, basal shoot diameter, length and width of the largest leaf of each plant. In addition, the following parameters were measured after each harvest: number of leaves on the main shoot, number of stipules together with branches (branches arise from stipules), length of the longest branch, number of new rhizomes, length of the longest new rhizome, leaf area of each plant (including leaf area of leaves on the main shoot, stipules and branch leaves and young rhizome leaves). Each sampled plant was divided into its organs. All samples were oven-dried at 85 °C to constant weight. Leaf area of each individual plant was measured with a ScanJet Plus Scanner (Hewlett Packard Company).

In the following text lateral shoots are referred to as branches, inflorescence and infructescence grouped together as inflorescence and new rhizome together with their apical above-ground parts, which form new shoots in the following spring, described as rhizome. New rhizomes are defined as rhizomes created during the observed growing season (see "Architecture of shoot and rhizome system" and Fig. 1). Both new and old rhizomes can be found in older plants (Fig. 1), but in our plants grown from seeds during a single season, only new rhizomes were present.

Data analysis

The following analyses were used for different characteristics and relations: two-way ANOVA with interactions to test effects of harvests and treatments. Where appropriate, log-transformation was applied to the primary data to achieve normality (Tables 1 and 2). The effect of harvest (i.e. time) lead usually to the trivial conclusion that some variable changes over time. Nevertheless, the significance of treatment and of interaction of treatment x harvest was of interest. The significant interaction term reveals that the differences among treatment change over time. If the interaction term is not significant, then the differences among treatments could be considered constant over time. Note that in the case of log-transformed data this means, that the ratios of original values are constatnt over time.

The influence of various nutrient levels on the allometric relationships and plant architecture were tested within the framework of general linear models (Zar 1984). The SYSTAT package was used for all analyses (Wilkinson 1990).

Results

Biomass allocation

All the observed parameters showed pronounced seasonal fluctuation and differed between nutrient treatments (Table 1, Fig. 2). The biomass allocation was significantly affected by nutrient supply: with increasing nutrient supply, relatively less biomass was allocated to below-ground parts (Fig. 2), so that the R/S (root/shoot) ratio is also affected (Table 1-No. 4, Fig. 3).

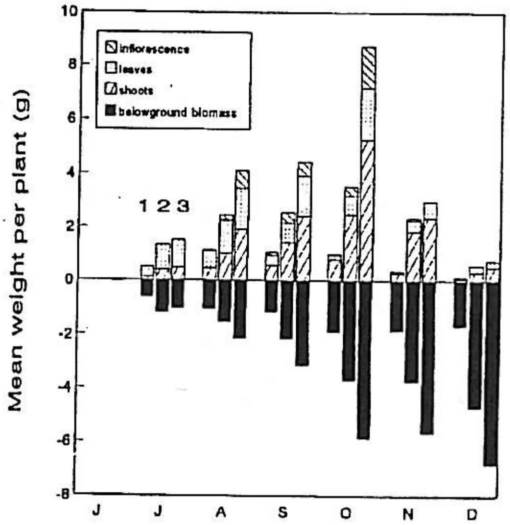

Fig. 2. Changes in biomass partitioning (g) in individual plants with different nutrient supply (1 - 75 kg NPK, 2 - 225 kg, 3 - 375 kg.ha^{-1}) over time (June to December).

Table 1. Results of two-way ANOVA with interactions

Response (dependent variable)	Log-tranformation of primary data	Source of variation	Harvest number	DF	*F*-ratio	*p*
1. total dry weight	+	harvest	1 to 7	6	800.22	<<0.01
		treatment		2	52.79	<<0.01
		harvest x treatment		12	2.25	<0.01
2. above-ground dry weight	+	h	1 to 7	6	492.20	<<0.01
		t		2	69.83	<<0.01
		h x t		12	3.71	<<0.01
3. below-ground dry weight	+	h	1 to 7	6	785.43	<<0.01
		t		2	27.44	<<0.01
		h x t		12	1.76	NS
4. R/S ratio	-	h	1 to 7	6	15.91	<<0.01
		t		2	6.86	<<0.01
		h x t		12	2.42	<0.01
5. shoot dry weight	+	h	1 to 7	6	685.40	<<0.01
		t		2	78.43	<<0.01
		h x t		12	4.85	<<0.01
6. leaf dry weight	+	h	1 to 7	6	256.82	<<0.01
		t		2	46.77	<<0.01
		h x t		12	3.76	<<0.01
7. leaf area	+	h	1 to 7	6	214.75	<<0.01
		t		2	31.43	<<0.01
		h x t		12	3.63	<<0.01
8. inflorescence dry weight	+	h	1 to 7	6	20.49	<<0.01
		t		2	24.27	<<0.01
		h x t		12	7.80	<<0.01
9. new rhizome dry weight	+	h	1 to 7	6	40.25	<<0.01
		t		2	24.62	<<0.01
		h x t		12	6.55	<<0.01
10. inflorescence dry weight/ new rhizome dry weight ratio	+	h	3 to 5	2	15.95	<<0.01
		t		2	3.72	<0.05
		h x t		4	1.83	NS
11. plant height	-	h	1 to 7	6	78.89	<<0.01
		t		2	35.23	<<0.01
		h x t		12	3.89	<<0.01
12. plant height	+	h	1 to 7	6	592.08	<<0.01
		t		2	31.70	<<0.01
		h x t		12	1.71	<0.1
13. number of new rhizomes	-	h	2 to 7	5	62.74	<<0.01
		t		2	8.41	<<0.01
		h x t		10	2.17	<0.05
14. length of longest new rhizome	-	h	3 to 7	4	7.14	<<0.01
		t		2	5.86	<0.01
		h x t		8	1.25	NS

NS...not significant, + transformed, - non-transformed.

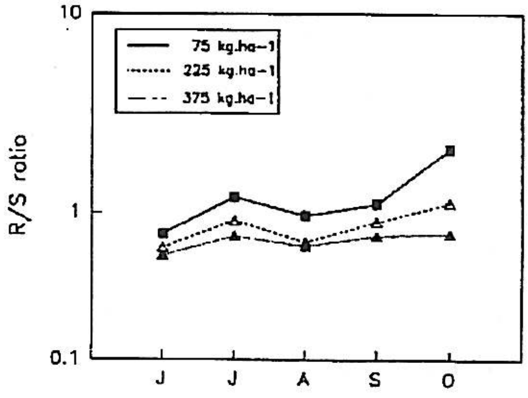

Fig. 3. Changes in R/S ratio with different nutrient supply of the first five harvests (June to October).

Both above- and below-ground biomass increased regularly up to the fifth harvest (October 10). Thereafter the above-ground biomass decreased, whereas the increase of below-ground biomass continued (Fig. 2).

The dynamics of above-ground biomass production was also affected: the higher the nutrient supply, the longer an intensive production of above-ground biomass lasted. This is reflected by a statistically significant interaction term in the majority of ANOVAs (Table 1-No. 2). As log-transformation was used, these results reveal that the ratios between the biomass values in individual treatments are not constant. In contrast, the ratios of below-ground biomass seem to be constant.

Similarly, for inflorescences, increasing nutrient supply increased their maximum weight and delayed their appearance (the higher the maximum weight and the later they appear; Fig. 2 and 4).

Changes of the architecture of individual plants and allometry of plant organs

Plant height was affected by the treatments (Fig. 4), the more nutrients, the higher plants. When log-transformation was applied to the data, the interaction term between time and treatment was not significant (Table 1-No. 12). This means that the ratios of plant heights in particular treatments are statistically constant over the time. Plant height was not affected by sex (Table 2-No. 2).

Inflorescence weight was positively correlated with plant height also within treatments and harvests (partial correlation coefficient = 0.365, $p<<0.01$). The nutrient enrichment (treatment) affected the relationship between plant height and inflorescence biomass; the slope of the regression of log inflorescence biomass on log plant height increases with nutrient enrichment. This means that the plants grown with higher nutrient addition are not only higher, but at the same height, they have higher inflorescence biomass (Fig. 4). A similar relationship was not significant for plant height and rhizome biomass (partial correlation coef. = 0.094, NS).

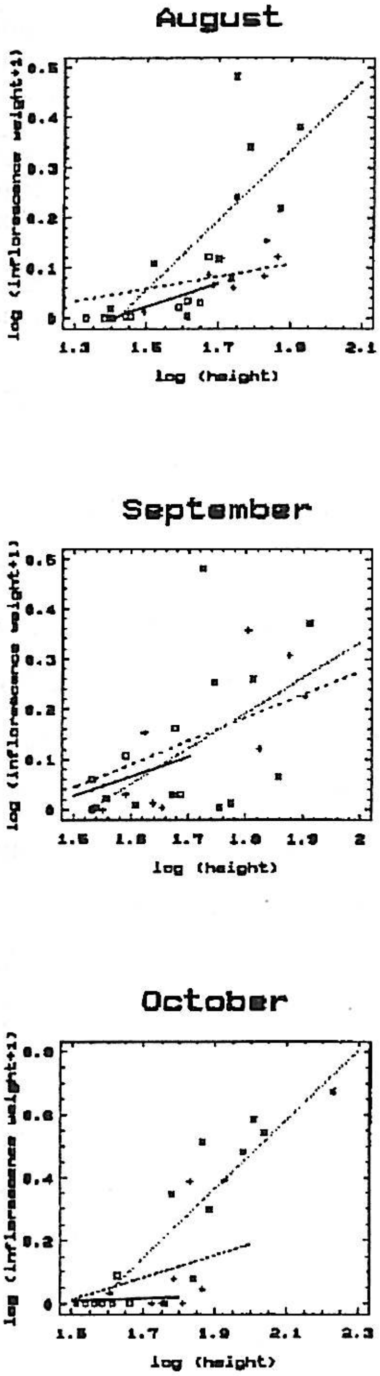

Fig. 4. Relationship between inflorescence biomass and plant height under various treatments at three harvests. Symbols: □ —— treatment 1 (75 kg.ha^{-1}); + ------treatment 2 (225 kg.ha^{-1});
✱ ················ treatment 3 (375 kg.ha^{-1}).

Table 2. Results of three-way ANOVA without interactions

Response (dependent variable)	Log-tranformation of primary daty	Source of variation	Harvest number	DF	*F*-ratio	*p*
1. number of branches on sex of shoots	-	treatment	3 to 6	2	3.35	<0.05
		harvest		3	6.85	<<0.01
		sex		1	0.08	NS
2. plant height on sex	-	treatment	3 to 6	2	10.98	<<0.01
		harvest		3	4.04	<0.01
		sex		1	3.69	<0.1

NS...not significant, + transformed, - non-transformed.

Branching of the main shoots (number of lateral branches) was correlated with plant height and changes with time (Fig. 4). Nevertheless, with constant plant height and harvest time, the differences in the number of branches among treatments were not significant (in general linear models analysis, corresponding $F = 1.20$, $p > 0.05$). This means that nutrient supply supports mainly growth in height while the number of branches corresponds to plant height and harvest time; there is no additional effect of nutrients. The number of branches was not affected by sex.

Number of new rhizomes was affected by both treatment and harvest, especially in older plants. No rhizomes were present at the first and the second harvests (Fig. 4). Differences among young plants were negligible in comparison with differences among mature plants (Table 1-No. 13). The length of the longest new rhizome changes with time and differs between treatments and harvests, especially so at the last three harvests (Table 1-No. 14, Fig. 4). Both the number of new rhizomes and length of the longest new rhizome increased with higher fertilization (Fig. 4).

Reproductive allocation versus clonal growth

The ratio of inflorescence biomass to new rhizome biomass is taken as measure of allocation to generative-vegetative reproduction. As the ratio is difficult to treat statisticaly (it is highly skewed, ranges from 0 to infinity) we used the transformation:

$$\frac{\text{inflorescence - new rhizomes biomass}}{\text{inflorescence + new rhizomes biomass}},$$

which is a simple transformation of the ratio of inflorescence to new rhizome biomass: ((1 - ratio)/(1 + ratio)), ranges from 1 (allocation to generative reproduction only) to -1 (allocation to vegetative reproduction only), and is symmetric. The ratio changes with time (harvest) and also with treatment. Nevertheless, the differences are constatnt over time (note the non-significant interaction).

The relationship between inflorescence biomass and total above-ground vegetative biomass is positive and is affected both by both treatment and harvest.

Positive effect of nutrient enrichment on inflorescence and new rhizome production was proved (see "Biomass allocation").

Discussion

The present study deals with *Urtica dioica* plants from unmanaged meadows of the Lužnice River floodplain. *Urtica* is generally sensitive to regular and frequent mowing (van der Maarel 1980), as only in unmown places a fast spread is observed (Prach *et al.* 1990; Šrůtek 1993). Its seedlings are frequently found also in mown floodplain meadows (Klimešová, in press) and have high potential for spread in unmanaged meadows. High soil nutrient content and sufficient soil moisture support strong competitive ability and expansion of *Urtica* (Grime *et al.* 1989). The pronounced increase in biomass with nutrient additions is typical of this species (Table 1, Fig. 2). Rorison (1968) has also found an almost linear positive response of *Urtica* to phosphate supply. Under fertile conditions high production of above-ground biomass and, therefore, high density of herbaceous litter also enable this species to compete successfully with most other herbaceous species (Al-Mufti *et al.* 1977).

The biomass allocation to above- and below-ground parts and to individual organs differed between treatments. (Table 1, Fig. 2). The highest R/S ratio was found with low nutrient supply (Fig. 3), as expected (Fitter and Hay 1991). In most cases the differences between treatments increase with plant age (Table 1).

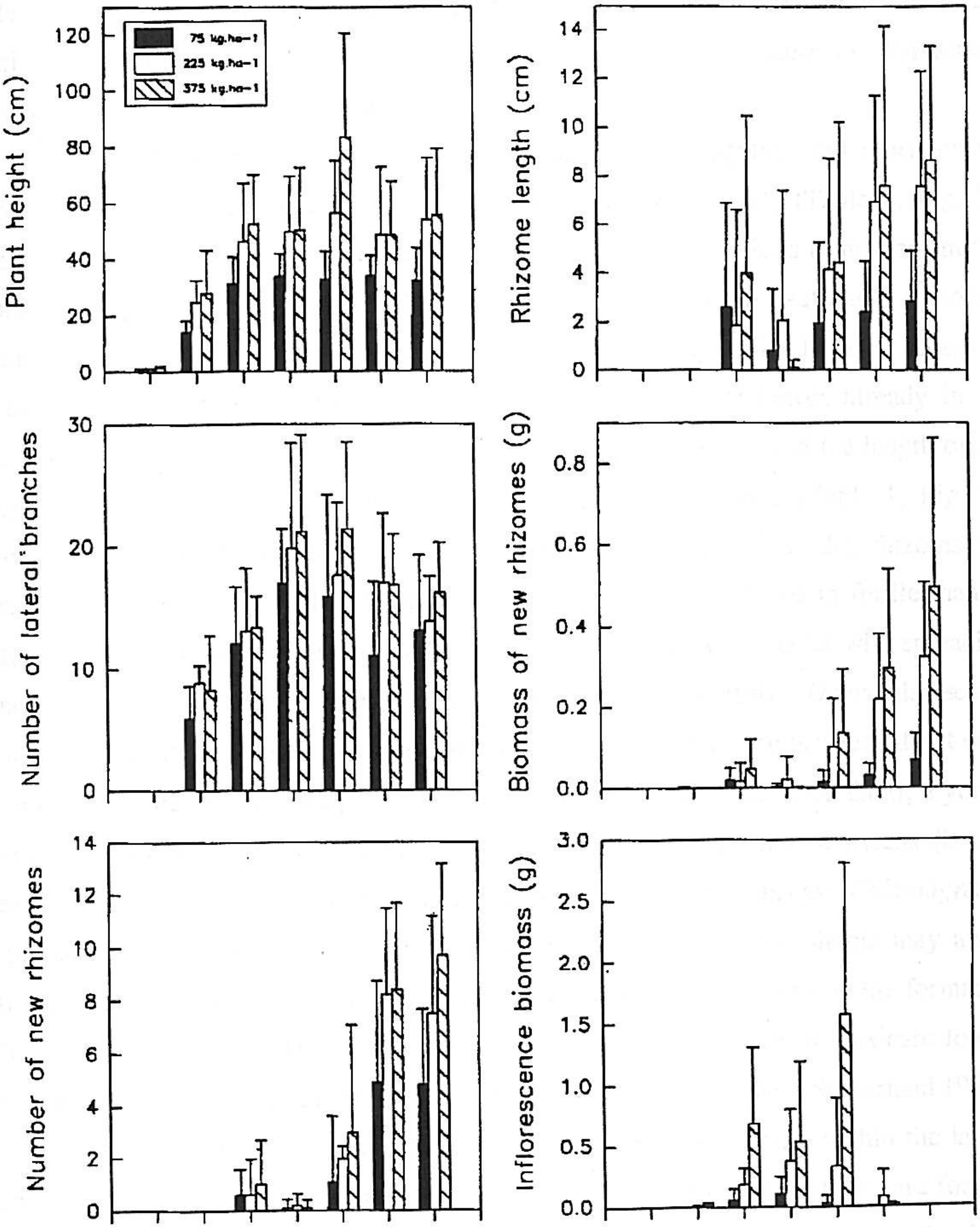

Fig. 5. Variation of the selected characteristics of growth and development of individual plants with different nutrient supply over time (June to December).

The biomass allocation to above- and below-ground parts and to individual organs differed between treatments. (Table 1, Fig. 2). The highest R/S ratio was found with low nutrient supply (Fig. 3), as expected (Fitter and Hay 1991). In most cases the differences between treatments increase with plant age (Table 1).

The formation of organs serving either vegetative propagation and reproductive allocation is strongly enhanced under conditions of high soil fertility (Table 1, Fig. 5). Production of new rhizomes increased in the autumn (Fig. 5). This is a mechanism for rapid early spreading of *Urtica* in the spring because many of its autumnal rhizomes resume their growth to produce new shoots very quickly (Greig-Smith 1948). The apices of these autumnal rhizomes frequently form terminal rosettes of leaves already in the autumn. Under more fertile conditions the number of new rhizomes and the length of the longest new rhizome are higher than with lower amount of nutrients (Table 1, Fig. 5). This result does not support the prediction of Schmid and Bazzaz (1992) that rhizomatous perennials should have a higher rhizome number but shorter rhizomes in fertile than in unfertile soil. Their prediction is supported by *Aster lanceolatus,* a species with spreading genet architecture ("guerrilla" growth form, sensu Lovett Doust 1981). *Urtica* also seems to follow "guerrilla" strategy. The growth pattern of its new rhizome is affected not only by soil fertility but also by competition. For example (Šrůtek, unpublished data), a young sparse clone establishing itself within a dense stand of *Calamagrostis canescens* (in wet meadows) spreads relatively fast by numerous long rhizomes. In this case *Calamagrostis* is probably not as strong competitor as *Urtica* and *Urtica* scaterred shoots may avoid intraspecific competition. Moreover, most of the rhizomes are successful in the formation of mature shoots in the next year after the establishment of the clone. In this case longer rhizomes can probably also evade the resource-depletion zone (compare Sutherland 1987). A similar situation is found at the edge of large old clones. However, within the larger clone the formation of short rhizomes does not prevail. Numerous new shoots are formed from short rhizomes in spring, but many of them die because of intraspecific competition (i.e. the density in April and October is 400-700 and 100-200 shoots per m^2, respectively; Šrůtek, unpublished data).

Under fertile conditions production of reproductive organs flowers and fruits) increased (Table 1, Fig. 2, 4). *Urtica* produces as many as 10,000 to 20,000 seeds per individual (Bassett et al. 1977; for *U. d.* L. ssp. *gracilis* (Ait.)Selander) with long-term viability in the soil (Ødum 1978) and mean germination rate of seeds of different populations from 50 to 70 %. The germination is negatively affected by flooding (Wheeler 1981).

The relationship between inflorescence biomass and total biomass is significantly positive. This result partly seem to correspond with Reekie and Bazzaz (1987b) who found that reproduction did not reduce the overall growth of *Agropyron repens*. Both direct photosynthesis by the reproductive organs and reproductive enhancement of leaf photosynthesis contributed to enhanced growth (Reekie and Bazzaz 1987a). However, photosynthetically active floral organs may not accurately reflect the cost of sexual reproduction of the plant (Weaver and Cavers 1980).

The positive correlation of generative reproduction with plant size, which was documented by the experiment, corresponds with earlier findings (Weaver and Cavers 1980; Hartnett 1990). The plants of the same height devote more to reproduction if grown in nutrient rich soil in the experiment.

Some structural relations do not follow known facts. The plant height and number of branches did not differ between male and female plants (Table 2). Generally, size differences between female and male individuals are documented within many species (Gross and Soule 1981; Lovett Doust and Lovett Doust 1987). Females are usually larger and form greater number of ramets than males. Lovett Doust and Lovett Doust (1987) found for *Rumex acetosella* that a female plant is able to retain leaves on existing ramets and to make more ramets, hence more leaves that live longer. Greater branching of female than male individuals has been reported for *Spinacia oleracea* plants by Onyekwelu and Harper (1979).

However, in the present investigation, branching (number of lateral branches) was correlated only with plant height and plant age but not with sex. High fertility did not affect the number of branches directly (Table 2, Fig 4). Plant height was affected by fertilizer-treatment and with harvest (Table 2). With regard to branching the overall plant size, but not the architecture was affected by fertilization. The increased number of lateral branches is important especially in late summer and autumn, when leaves of the branches live longer and hence may produce reserve assimilates. Likewise the leaf rosettes of autumnal new rhizomes may also produce extra reserves.

It may be concluded that nutrient enrichment supports the competitive ability of the life strategy of *Urtica dioica* (compare Grime *et al.* 1989). High nutrient uptake from the soil increases especially the allocation of biomass to reproductive organs and those vegetative organs which are important for vegetative spreading of established *Urtica* clones and for the growth of seedlings colonizing mainly disturbed places.

Acknowledgements

The author is especially indebted to Dr. J.Š. Lepš (University of South Bohemia, České Budějovice, Czech Republic) for his help with data processing and to Dr. Jan Květ (Institute of Botany, Třeboň, Czech Republic) for his valuable comments and linquistic advice on the manuscript. The introductory figure of Urtica dioica was drawn by Dr. J. Klimešová and Mrs. L. Kučeravá. The work was supported by the grant No. 60539 of the Czech Academy of Sciences: Invasive plant populations in eutrophic habitats.

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chapter 4

GROWTH RESPONSES OF *URTICA DIOICA* L. TO DIFFERENT WATER TABLE DEPTH

Growth responses of *Urtica dioica* L. to different water table depth

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Acta Oecologica, submitted

Abstract

The study examined the effect of various levels of water table depth (WTD) on production, biomass allocation, allometric relationships and transpiration rate in *Urtica dioica* during one growing season. The water table depths were as follows: 60, 50, 40, 30, 20, and 10 cm under the soil surface. There were established by the six different heights of substrate in laminate containers: 80, 70, 60, 50, 40, 30 cm. The height of the constant WTD was 20 cm. Urtica dioica individuals were established from apical parts of young rhizomes and planted in a regular grid 15 cm apart, 5 by 6 saplings per container. The height of all individuals and the length and width of the biggest leaf blade of each individual were measured in three times; transpiration rate was measured in two times during the experiment. Above-ground biomass of all individuals was harvested at 24th July. It was divided to individual organs; different biometric parameters were measured.

All the biometric characteristics were highly dependent on WTD. With the water table comming closer to the soil surface, biomass was lower, the plants were lower, had less branches and rhizomes, and the rhizomes were shorter. Most allometric relationships were affected by water level (particularly those between plant height and other characteristics such as basal diameter, length of longest branch and rhizome); the biometric parameters were highly dependent on the plant height. Transpiration of plants strongly decreased with decreasing WTD.

Keywords: above-ground biomass, allometric relations, biomass allocation, transpiration, *Urtica dioica*, water table depth.

Introduction

The wetland habitats in cultivated landscape have been significantly altered by human activities, particularly by agricultural practices (e.g. wetland drainage, canalization of streams and rivers, bank stabilization, livestock grazing, utilization of fertilizers and pesticides) and but also by management exclusion, particularly cutting (Mathias & Moyle, 1992).

In both cases the altered wetlands are the favourable areas for fast spread of highly competitive native plants or/and invasive plants. *Phalaris arundinacea, Calamagrostis canescens, Filipendula ulmaria, Urtica dioica, Glyceria maxima* are examples of these expansive native plants for the Central European wet meadows (Hlaváček & Pyšek, 1988; Prach *et al.*, 1990; Prach, 1992; Šrůtek, 1993); *Impatiens glandulifera, Rudbekia laciniata, Spiraea salicifolia* represent invasive plants (Šrůtek, 1993; Pyšek & Prach, 1994).

Urtica dioica, a native plant of the river or stream banks, frequently forms large patches or stands in higher parts of microtopography and/or shallow depressions within floodplains (Prach, 1992; Šrůtek, 1993). Its spread in wet meadows is also affected by frequency and length of inundation (Klimešová, 1994). This species has no special adaptation to anoxic conditions in the flooded soils (Grime *et al.*, 1989). Therefore, its fast spread in the flooded areas usually occurs during a climatically dry period. Not only fast vegetative growth of older clones of *Urtica* but also a great amount of seeds in the area (hight seed production and soil seed bank) enables the successful occupation of disturbed parts of wetlands (Klimešová, 1995). Floods significantly reduce the survival of young plants of *Urtica*. The effect of floods on the older plants is not so strong, resulting only in their lower biomass (Klimešová, 1994).

This study examines the effect of various levels of water table depth on the production and pattern of biomass allocation within *Urtica* plants during one growing season. The following questions were addressed:

(1) What is the influence of various levels of water table depth on biomass allocation

within the plants?

(2) What are the consequences of different water table depth on plant architecture and allometry of various organs?

(3) Are there any changes in transpiration of plants under different soil-moisture conditions?

Material and methods

Experimental design

The *Urtica dioica* individuals were planted in the laminate containers (200 x 100 x 40 cm) which were filled with sandy loam (loam:sand = 3:1) and located in the institute's garden in the spring, 1990.

The regular shape of each experimental plot in a container was arranged by wooden walls of the same height as substrate height. The six levels of water table depth (WTD) was established by six different height of substrate, i.e. 80, 70, 60, 50, 40, 30 cm. The height of the constant WTD was 20 cm. It was kept by the simple overflow and barrel with water in each container. The substrate was homogenously irrigated by the system of the regularly arranged pipes on the container bottom.

The combined NPK fertilizer (12.5 % N, 8.5 % P, 16 % K) was applied in the dose of 28 g of fertilizer per m^3 of substrate applied as a water solution three times during the experiment (28th May, 20th June and 13th July).

The terminal parts of a new rhizomes (10 to 15 cm in length, with 2 to 4 nodes and terminal green rose of young leaves) for establishment of plant individuals were collected on March 23th from one natural clone of Urtica found within unmanaged floodplain meadows. These meadows are situated in the Lužnice River floodplain near the border with Austria, in the Třeboň Biosphere Reserve, South Bohemia, Czech Republic (Prach *et al.*, 1990; Šrůtek, 1993).

Rhizome pieces were arranged in a regular grid 15 cm apart on May 8th. Thirty individuals were planted in each container (5 by 6 plants).

The above-ground edge effect was removed by one row of plants allocated around the rectangular plot in each container. This row was separated in the soil from the plot by

PVC sheet.

The height of all individuals in each container was measured three times during the experiment on the following dates: 13th June, 29th June, 24th July. The length and width of the biggest leaf of each individual were measured at the same time.

The transpiration rate of randomly selected ten individuals for each WTD was measured two times during the experiment (on 27th June, and 23th July) using steady-state porometer (LI-1600 for measurement of direct readout of transpiration rate and stomatal conductance; LI-COR, Lincoln, Nebrasca). The third or fourth couple of leaves from the top of shoot was selected for measurement.

The following parameters were measured after harvest at 24th July: plant height, basal diameter of shoot, number of leaves on the main shoot, number of stipules together with branches (branches growing from stipules), number of branches, length of the longest branch, number of rhizomes, length of the longest rhizome. Each sampled plant was divided into its organs. All samples were oven-dried at 85 °C to constant weight.

In the following text lateral shoots are referred to as branches, inflorescence and infrutescence grouped together as inflorescence and new rhizome together with their apical above-ground parts, which form new shoots in the following spring, described as rhizome. New rhizomes are defined as rhizomes created during the observed growing season. Both new and old rhizomes can be found in older plants (at least two years old). In our case, only new rhizomes were present, as well as the rests of rhizome pieces used for establisment of plant individuals.

Data analysis

Simple linear regression was used to reveal the dependence of particular biometric and biomass characteristics on the WTD (Zar, 1984).

The influence of WTD on allometric relationships was tested using multiple linear regression. If the WTD significantly influences the allometric relationship between X and Y (i.e., $Y=a+bX$), then the partial regression coefficient b_2 in the equation $Y=a+b_1X+b_2\,\mathrm{WTD}$ is significantly different from zero. Note that because the allometric relationship usually takes the form of a power curve, X and Y are biometric characteristics subjected to log-transformation (Zar, 1984).

Transpiration was measured twice on the same plants. The length and width of leaves and plant height were measured three times. Consequently, repeated measurement analysis was applied in these cases.

Where appropriate, log-transformation ($\log(x+1)$ when data contained zeros) was applied to the primary data to achieve normality.

The SYSTAT and STATGRAPHICS packages were used for analyses (Wilkinson 1990).

Results

Dependence of biomass allocation and biometric parameters on the water table depth

All the biometric characteristics were highly dependent on the WTD; the plants were lower, had less branches and rhizomes, the rhizomes were shorter and the biomass was lower with the water table coming closer to the soil surface. Generally, the statistical relationships were very significant (Table 1, Fig. 1).

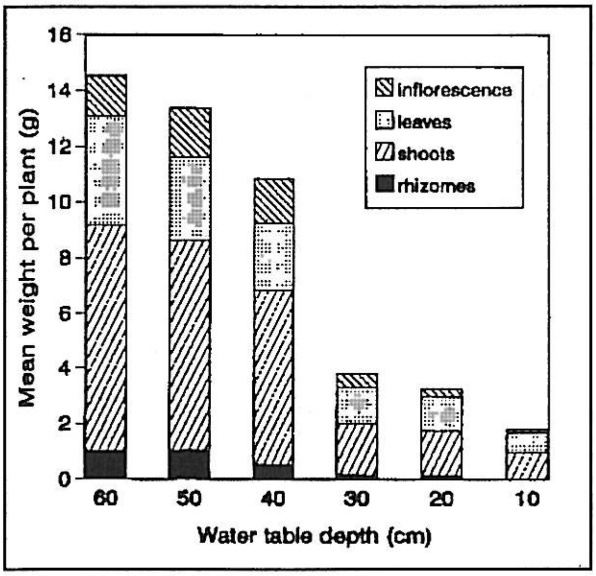

Fig. 1. Biomass partitioning (g) in individual plants in different water table depth (from 60 to 10 cm under soil surface) at the end of experiment.

Table 1. Results of linear regression between water table depth (cm belowground) and selected parameters. All the regressions were statistically highly significant ($P < 0.01$).

Resource (dependent variable)	Log-transformation of dependent variable	Intercept	Slope	R^2
total aboveground biomass	+	0.062	0.185	0.652
shoot biomass (including branches)	+	-0.259	0.204	0.668
leaf biomass	+	-0.279	0.139	0.584
branch biomass	+	-0.743	0.188	0.368
inflorescence biomass	+	-0.031	0.077	0.42
rhizome biomass	+	-0.068	0.056	0.315
plant height	+	1.629	0.088	0.63
basal diameter	+	0.606	0.052	0.53
number of leaves on main shoot	-	6.35	0.684	0.259
number of branches	-	10.808	0.75	0.177
number of rhizomes	-	0.229	0.309	0.205
length of longest branch	+	0.253	0.227	0.391
length of longest rhizome	+	0.284	0.219	0.437

In particular, a decrease in shoot biomass was dramatical. It is most pronounced at a WTD of 30 cm under the soil surface. Leaf biomass decreased continuously with higher groundwater table (Fig. 1). Within treatments variability among individual shoots was relatively low in the all above-mentioned characteristics. Inflorescence biomass did not respond so rapidly at deeper groundwater table (60, 50 and 40 cm under the soil surface; Fig. 1). Even if the water table was 50 and 40 cm deep, the inflorescence mean dry weight was rather higher than in 60 cm. Variability among shoots was high. Branch and rhizome biomass responded in the similar way.

As expected, the characteristics measured on three dates (plant height, length and width of leaves) changed with time, differed between variants and the differences increased with time (repeated measurement analysis, $P << 0.01$ in all the parameters).

Relationships between various parameters affected by water table depth

Allometric relationships were mostly affected by water level (particularly those between plant height and other characteristics: Fig. 2, Table 2), and obviously, the biometric parameters were highly dependent on the plant height. Generally, where the plant height was treated as the first independent variable, the b_2 coefficient (partial regression coefficient for WTD) was positive, indicating that biometric characteristics (basal diameter, length of the longest branch and rhizome, inflorescence biomass etc.) increased with depth water level for the same plant height (Fig. 2, Table 2). The relatioship between plant height and shoot branching (number of branches) was not affected by WTD, but branch biomass was increased under drier conditions for the same plant height. The number of rhizomes was related to the total above-ground biomass but not to plant height; rhizome biomass was positively correlated with plant height and increased with WTD.

Relationship between reproduction (inflorescence biomass) and vegetative spread (rhizome biomass) was significant.

Plant height was related to leaf shape (expessed by leaf length/leaf width ratio) only in young plants at the first measurement (13th June). The ratio increased with plant height, but the relationship was independent of WTD. At the other two measurements, this relationship was not significant.

Table 2. Partial regression coefficients for water table depth (WTD) in the equation $Y = a + b_1X + b_2\mathrm{WTD}$ and their significance.

Dependent variable (Y)	Independent variable (X)	Log-transformation of primary data	Partial regression coefficient for WTD (b_2)	SE of b_2	Significance level of b_2
basal diameter	plant height	+	0.026	0.011	0.0144
length of longest branch	plant height	+	0.334	0.078	0.0000
length of longest rhizome	plant height	+	0.189	0.076	0.0135
number of branches	plant height	-	0.233	0.445	0.6036
number of rhizomes	plant height	-	0.334	0.173	0.0545
number of rhizomes	total above-ground biomass	-	0.428	0.146	0.0038
number of branches	total above-ground biomass	-	0.736	0.383	0.0558
total above-ground biomass	plant height	+	0.105	0.024	0.0000
leaf biomass	plant height	+	0.122	0.028	0.0000
branch biomass	plant height	+	0.237	0.067	0.0006
inflorescence biomass	plant height	+	-0.01	0.019	0.6003
rhizome biomass	plant height	+	0.063	0.023	0.0060
rhizome biomass	total above-ground biomass	+	0.226	0.120	0.0614
inflorescence biomass	rhizome biomass	+	0.129	0.018	0.0000

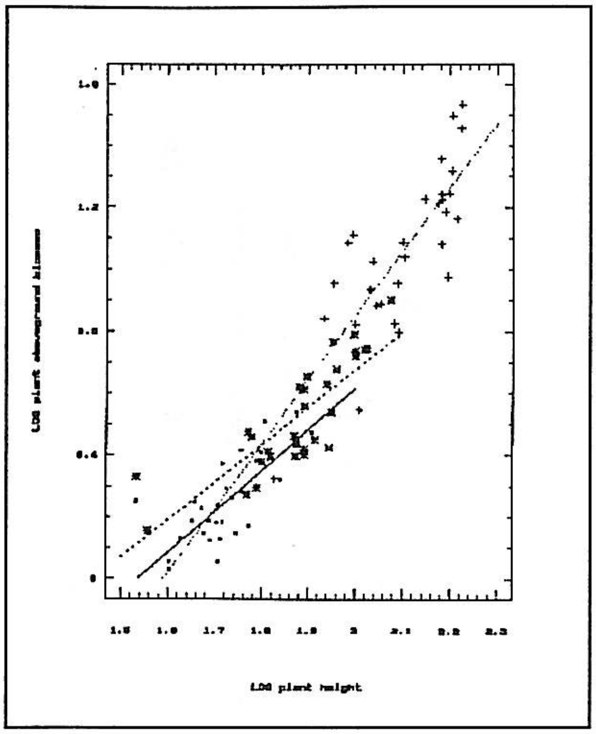

Fig. 2. Relationship between plant height and above-ground biomass on the three water table depth (WTD): + ·················· 60 cm,✱ ------30 cm,□———10 cm under soil surface.

Transpiration under different water table depth

Transpiration of plants was strongly affected by water level at both the measurements; traspiration rate decreased with the decreasing WTD (Fig. 3).

Discussion

The wetlands and particularly floodplains are one of the most important habitats for *Urtica dioica* in Central Europe (Ellenberg, 1988). Although *Urtica* has probably no important anatomical and morphological adaptations to conditions of permanent inundation (Grime *et al.*, 1989; Končalová, 1990; Crawford, 1992), it is able to occupy large areas of unmanaged wetlands. As other terrestrial plants in wet habitats, *Urtica* prefers elevated places and shallow depressions (Šrůtek, 1993). Voesenek *et al.* (1993) described a similar distribution of *Rumex acetosa* in the floodplain of the Rhine delta. *Urtica* seedlings tolerate short-term flooding in spring and summer but its rapid spread is supported by a drier

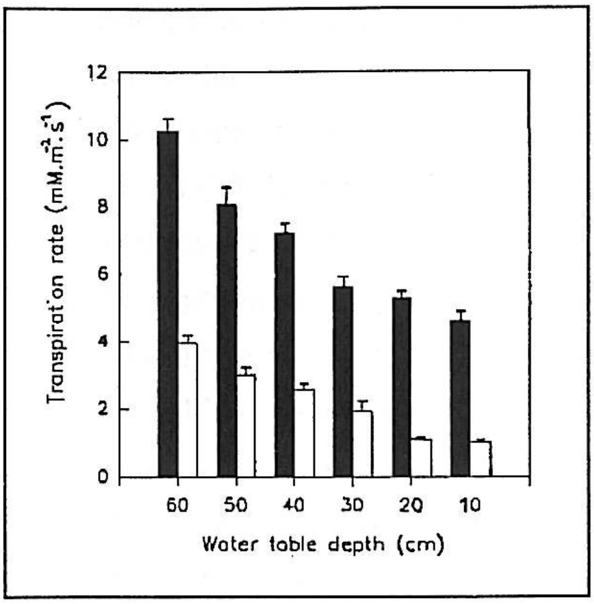

Fig. 3. Transpiration rate (mM.m^{-2}.s^{-1}) of individual plants in different water table depth (from 60 to 10 cm under soil surface) in the two measurement during the experiment

growing season (Klimešová, 1994). Generally, the consequences of flooding for plants depend on the stage of their ontogenetical development, e.g. stem height, formation of root system, storage of nutrients and carbon (Ernst, 1990). Furthemore, common characteristics of species well adapted to flooding are increases in root porosity and associated decreases in specific gravity and activation of anaerobic metabolism (Carter & Grace, 1990). Probably, only spatial arrangement of the rhizome and root layer (it forms 10-15 cm thick well aerated layer of intertwined rhizomes and roots in the topsoil with big volume of litter and detritus)(Šrůtek, unpublished field observation) and accumulated storage material in rhizomes and roots of mature plants enable *Urtica* to survive several weeks under water. However, *Urtica* plants, particularly seedlings, are severely injured (Klimešová, 1994). *Urtica* seedlings respond in a different way to spring and summer flooding. In summer, seedlings show degradation of roots, ceassation of dry mass accumulation and growth, shedding of leaves and inflorescences and growth of adventitious roots on submerged stem parts, which substitute a deep rooting system (Klimešová, 1994; Ernst, 1990). The youngest seedlings survive the spring flood, but post-anoxic injury affects their mortality (Klimešová, 1994). Frequently, seedlings of terestrial plants show no growth under anoxia. For example, Fagerstedt & Crawford

(1987) refered anoxic (by ethanol production) and post-anoxic injury (by acetaldehyd production) of *Hordeum vulgare* seedlings under flooding conditions.

The present study evaluted responses of above-ground organs of *Urtica dioica* to different water table depths (WTD) (60, 50, 40, 30, 20 and 10 cm under ground). The answers to the introductory questions are the following:

(1) Standing crop of above-ground parts (i.e. total biomass, shoot, leaf, branch, inflorescence and rhizome biomass) was strongly affected by changes in WTD (Fig. 1, Table 1). Van der Sman *et al.* (1988) documented similar results for *Chenopodium rubrum*, biomass of which was severely reduced in response to waterlogging.

Therefore, the competitive ability of *Urtica* decresed with increasing WTD. It is characterized by the effect of low WTD on the features important for the competitive ability (Grime *et al.*, 1989). For example, a consequence of a decrease in above-ground biomass, particularly the shoot biomass (Fig. 1, Table 1), is a low production of litter, which is important for competitive exclusion of weak species (Al-Mufti *et al.*, 1977). In our case, those could be e.g. *Ficaria verna, Anemone nemorosa,* spring geophytes common in rather monospecific stands of *Urtica.*

Similar effect of flooding on biomass production were described by Salo (1989) on *Trifolium pratense* and *T. hybridum.* These species gave the lowest relative yield after flooding compared to the investigated grasses such as *Phalaris arundinacea, Alopecurus pratensis, Festuca pratensis* etc. Waldren *et al.* (1988) showed a reduction of total dry weight and dry weight of individual organs of *Geum urbanum* by flooding. Orchard & Jessop (1984) showed that waterlogging periods of only three days can result in marked reductions in leaf area and yield of *Helianthus annuus* and *Sorghum bicolor.*

Reproductive effort (biomass of male and female inflorescences) was also suppressed by low WTD (Fig. 1). However, this negative response was negligible at the low groundwater table (60, 50, 40 cm under ground). A severe decrease in inflorescence mass was observed in a water level of 30 cm under ground. Therefore, the success of generative reproduction of *Urtica* in frequently flooded areas decreases by low seed production but also probably by short viability of seeds under wet conditions. Hook (1984) reported that the majority of land plant seeds lose their viability if submerged for prolonged periods.

(2) *Urtica* decreased shoot height with higher soil moisture (Table 1), as well as

length of the longest branch and rhizome, and also the number of branches and rhizomes decreased with lower WTD..

In the field, higher number of *Urtica* branches will probably result in prolongation of period of assimilate storage; in autumn, shoots fall down and shoot branches become erect, forming additional shoots able to continue photosynthesis. Therefore, further assimilates can be produced and transported to below-ground organs. These shoots frequently take root. On the contrary, in many aquatic and semi-aquatic plants, rapid shoot elongation in response to flooding was observed (Jackson & Drew, 1984; Van der Sman *et al.*, 1993). Van der Sman *et al.* (1991) observed in *Rumex maritimus* a shift from extension of petioles to extension of internodes and a decrese of the rapid elongation response upon flooding in the course of the development of flowering plants.

The WTD affected allometric relations between different organs (Fig. 2, Table 2). Obviously, the basal diameter, length of the longest branches and rhizomes, total above-ground biomass etc. were positively correlated with plant height. Nevertheless, the partial regression coefficients have shown that even if the plant height is kept constant, more robust plants showing a frequent shoot branching and a strong ability of rapid vegetative spread were observed in drier sites of the moisture scale (when water table was 60 cm under ground, in our case). Reproduction appeared to be even more influenced than biomass by waterlogging (Van der Sman *et al.*, 1988). Van der Sman *et al.* (1991, 1992, 1993) reported that seed output of *Rumex maritimus* was positively correlated with the number of stems and total stem length under drained conditions.

The inflorescence biomass and rhizome biomass were positively corelated, even within a level of WTD. In robust vigorous plants, a high production of seeds can be followed by successful vegetative spread of the same plant. Usually, only decrease in flower creation, flower and fruit abscission and fruit production is documented as plant responses to flooding (Hook, 1984; Crawley, 1986). Hutchings & Bradbury (1986) suggested that rhizome and stolon extension may not necessary constrain growth and development elsewhere in the plant. Reekie (1991) suggested the following general premise in relationship between seed production and vegetative propagation: plants minimize the overall cost of propagation by preferentially allocating resources to the mode of propagation that minimizes the detrimental effects of propagation upon growth.

The relationship between plant height and leaf shape (leaf length/leaf width ratio) is rather complicated. Young higher plants showed a tendency to form narrower leaves. The relationship was not affected by water level. This tendency was not observed in older plants. The relationship between leaf morphology and water availability is documented more frequently than effects of WTD on relationship between plant height (size) and leaf morphology. For example, change in leaf size is related to climatic zones (water availability); the largest leaves are found in tropical rain forest and small leaves in deserts, tundra or heathland communities (Crawley, 1986).

(3) Transpiration was negatively correlated with the level of groundwater table. The stressed plants under wettest conditions were lowest in transpiration rate, as usual (Fitter & Hay, 1991). Transpiration gradually increased with increasing of the WTD. This corresponds to the suggestion that stomatal closure and reduced leaf growth in herbaceous species may be the most rapid external plant response to flooding (Hook, 1984). Kozlowski (1984) suggested that stomatal closure is a consequence of reduction in soil oxygen.

Another response of *Urtica* plants to higher soil moisture during the experiment was chlorosis of leaves, observed visually (Šrůtek, personal observation). Usually, chlorosis is related to growth reduction of the above-ground parts and root system. Leaf senescence and absision follow (Jackson & Drew, 1984; Kozlowski, 1984). Van der Sman *et al.* (1988) suggested that especially in young plants with limited reserves, nitrogen deficiency is an early consequence of waterlogging and causes premature leaf senescence while mobile nutrients are reallocated from older leaves into younger ones.

In spite of a decreased competitive ability of *Urtica dioica* in regularly flooded wetlands, this species is able to persist in unmown wetlands for many years and form almost pure large stands. The main reasons are as follows: (1) preference and occupation of dried elevated places and shallow depressions, (2) competitive exclusion of the most of other species both mechanically (rhizomes show progressive vegetative spread and penetrating also through compact tussocks of wetland grasses) and chemically (allelopathic effects are documented), (3) high seed production, and (4) tolerance to short-term flooding.

Acknowledgements

The author is especially indebted to Dr. J.Š. Lepš (University of South Bohemia, České Budějovice, Czech Republic) for his help with data processing, his valuable comments and linquistic advice on the manuscript. The investigation was supported by the grant No. 60539 of the Czech Academy of Sciences: Invasive plant populations in eutrophic habitats.

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chapter 5

SHOOT GROWTH AND MORTALITY PATTERNS OF *URTICA DIOICA*, A CLONAL FORB

Shoot growth and mortality patterns of *Urtica dioica*, a clonal forb

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Annals of Botany, in review

Abstract

The growth and mortality patterns of the clonal forb *Urtica dioica* were investigated at the level of the individual shoot in two growing seasons, 1991 and 1992. Shoot height and diameter at ground level of each shoot tagged in spring were measured repeatedly five times during the growing season. Dry weights of these repeatedly measured shoots were estimated using an allometric relationship between dry weight, height and diameter of harvested shoots. A great decrease in shoot density occurred with stand development from the beginning of the growing season in both the years (shoot survival rate was about 30 % at the end of the growing season): (1) shoot mortality rate per 10x10 cm subplot between censuses was positively dependent on shoot density per subplot; (2) the mortality rate of individual shoots was negatively dependent on shoot size (height, diameter and weight) as a consequence of asymmetric competition between living and dying shoots; (3) shoot size (height, diameter and weight) variability in terms of the coefficient of variation and skewness decreased in accordance with shoot mortality. Regression analysis based on a model for individual shoot growth considering both one-sided and symmetric competition showed that competition between living shoots was almost absent. The mortality pattern of *Urtica dioica* indicates that shoot self-thinning occurred from the early growing stage as in non-clonal crowded monospecific stands, and contrasts with many clonal plants where shoot self-thinning rarely occurs or, if any, is confined only to later growing stages. The pattern of growth and competition between living shoots of *Urtica* *dioica* contrasts with non-clonal crowded plants undergoing intense competition (usually asymmetric) between individuals, but is a common feature of many clonal plants where shoot competition is supposed to be reduced by "physiological integration" between shoots. These form a new pattern not reported yet for clonal plants. A wide spectrum of the growth, competition and mortality patterns of shoots of clonal plants is pointed out. Some possible mechanisms for the pattern of *Urtica dioica* are discussed.

Keywords: Diffusion model, individual shoot growth, shoot competition, shoot self-thinning, shoot size variability, *Urtica dioica* L.

Introduction

The clonal dioecious forb *Urtica dioica* L. is native throughout Europe and Asia from the Mediterranean to the Arctic regions (predominantly in Europe; Greig-Smith, 1948). In Central Europe, Urtica dioica forms large stands, especially in open areas of river floodplains (Ellenberg, 1988). High soil moisture and nutrient content in the soil enable *Urtica dioica* to spread quickly. Moreover, many floodplain meadows abandoned in the past, particularly in Central and Eastern European countries, have supported the spread of *Urtica dioica* (Šrůtek, 1993). *Urtica dioica* suppresses many other plants and forms almost pure stands with low biomasses of other species under its canopy (Al-Mufti et al., 1977; Grime et al., 1989; Šrůtek,1993).

The present paper focuses on the seasonal shoot dynamics of *Urtica dioica* by investigating the processes of growth and mortality of individual shoots and the mode of shoot competition. The growth and mortality dynamics of non-clonal plants, especially artificial crowded monospecific stands, have extensively been studied at the level of the individual plant [for example, reveiws of Benjamin and Hardwick (1986), Weiner and Thomas (1986), Hara (1988) and Weiner (1990)]. However, the study of clonal plant dynamics at the level of the shoot and at the level of the clone is still in its infancy and controversial [De Kroon, Hara and Kwant, 1992; see also reviews of De Kroon (1993) and Hara (1994)], especially concerning the effect of "physiological integration" between shoots (Hutchings, 1979) on shoot growth and mortality. Physiological integration is defined as "the exchange of resources and growth substances between shoots of a single clone" [De Kroon and Kwant 1991; reviews of Pitelka and Ashmun (1985) and Hutchings and Slade (1988a, b)]. According to the hypothesis of physiological integration, smaller shoots (or shoots in the dark) are supported by the transport of resources from larger shoots (or shoots in the light), especially early in the growing season, resulting in the delay or absence of density-dependent shoot self-thinning, little competition between shoots and the decrease in shoot size variability (for example, Hutchings, 1979, 1983; Bradbury, 1981; Cain, 1990; Hara, van der Toorn and Mook, 1993). De Kroon and Kwant (1991) and De Kroon et al. (1992), however, did not find any effects of physiological integration at the level of the entire clone of *Brachypodium pinnatum* and *Carex flacca.* De Kroon (1993) and De Kroon and Kalliola (1994) suggest the occurrence of density-dependent shoot self-thinning over years in the clonal giant grass *Gynerium sagittatum.* Hutchings and Price (1993) refuted the commonly-quoted view that physiological integration between shoots of clonal herbs evens out the effects of variation in environmental quality, and promotes equitable shoot performance. This paper reports on a new pattern of shoot dynamics of *Urtica dioica* not reported yet for clonal plants, and points to a wide spectrum of the growth, competition and mortality patterns of shoots of clonal plants in comparison with those of non-clonals.

Materials and methods

Study site

This study was carried out in a *Urtica dioica* stand in the Lužnice River floodplain, 25 km SSE of the town of Třeboň, Czech Republic. The geomorphological description of the floodplain and the characteristics of past human activities in this area have been given by Prach, Kučera and Klimešová (1990) and Šrůtek (1993). The mean annual temperature and precipitation from 1988 to 1993 at the meteorological station of the Institute of Botany (situated about 400 m from the study site, 460 m a.s.l.) were 7.7 C and 606 mm. The study site was in the abandoned part of the floodplain near Halámky village and 30 m from the river bank. The floodplain meadows have not been mown for about 20 years. The study plots were situated in a dense and almost pure stand of *Urtica dioica.* The biomass of species other than *Urtica dioica* (in the understorey of *Urtica dioica*: *Ficaria* *verna, Anemone nemorosa, Galium aparine, Glechoma hederacea, Phalaris arundinacea, Cirsium palustre, Ranunculus repens, Angelica sylvestris* and *Alopecurus pratensis*) was almost negligible (usually between 0～5 % of the total biomass), and only the growth and mortality of *Urtica dioica* are analysed here.

Measurements

Four 1x1 m permanent plots were set up in April 1991, and each plot was divided into 100 10x10 cm subplots (400 subplots in total). 91 subplots were selected randomly from the total of 400 subplots (using a random number table) and all the shoots in the 91 subplots were tagged in April 1991. Shoot height and diameter at ground level of the tagged shoots were measured repeatedly on 11 April (census 1), 16 May (census 2), 12 June (census 3), 23 July (census 4) and 4 September (census 5) 1991. Shoots which emerged after census 1 in the 91 subplots were also tagged and measured. The number of shoots in all the 400 subplots were counted on these census dates. At the same time (or ±1-2 days), five 25x100 cm plots were harvested from five transects (one harvest plot from one transect) located near the permanent plots. The number of shoots was counted and the total dry biomass (85 °C for two days) was weighed for each harvested plot. Moreover, about 35 shoots were randomly selected in each harvested plot (about 175 shoots in total) and measured for shoot height, shoot diameter at ground level, leaf area, stem, leaf and inflorescence (or infructescence) dry weights. In addition to the harvests made on the same days (or ±1-2 days) of the repeated measurements in the permanent plots, harvests and sample measurements were also made on 28 April, 27 May, 30 June, 13 August, 6 October 1991.

The same method was applied to the same four permanent plots also in 1992. All shoots in the 91 subplots were tagged again in April 1992 (note that shoots of *Urtica dioica* die back in winter) and measured repeatedly for shoot height and diameter at ground level on 8 April (census 1), 13 May (census 2), 1 July (census 3), 23 July (census 4) and 1 October (census 5) 1992. The same sample measurements as in 1991 were made for five 25x100 cm harvested plots on the same days (or ±1-2 days) of the repeated measurements. In addition to these dates, a harvest and sample measurements were also made on 18 March 1992.

Hara (1984) proposed a size-structured stochastic model for the growth and size-structure dynamics of a single-species plant population ("diffusion model"):

$$\frac{\delta}{\delta t} f(t,x) = \frac{1}{2} \frac{\delta^2}{\delta x^2} [D(t,x)\, f(t,x)] - \frac{\delta}{\delta x} [G(t,x)\, f(t,x)] - M(t,x)\, f(t,x), \qquad (1)$$

where $f(t,x)$ is the size distribution function of size x at time t, $G(t,x)$, $D(t,x)$ and $M(t,x)$ are the mean of absolute growth rates, the variance of absolute growth rates and the mortality rate of individuals of size x at time t. The $G(t,x)$ and $M(t,x)$ functions represent the averaged size-dependent characteristics of species, whilst the $D(t,x)$ function represents variations in the species characteristics caused by environmental heterogeneity, genetic variation, variation in the neighbourhood competition effect due to spatial distribution pattern of individuals, etc. If the function forms of $G(t,x)$, $D(t,x)$ and $M(t,x)$ are known, the dynamics of size structure can be described mathematically.

Allometric relationships between shoot dry weight, w, [(stem weight)+(leaf weight)+(inflorescence weight)], shoot height, h, and shoot diameter at ground level, d, were obtained from the harvested shoots (about 150-175 shoots in total) at each time of repeated measurement in the permanent plots:

$$\log_{10} w = a + b \log_{10} h + c \log_{10} d, \qquad (2)$$

where a, b and c are time-specific parameters. Applying eqn (2), dry weights of repeatedly measured shoots in the permanent plots were estimated at each census in a growing season.

The $C(t,w)$ function was introduced to express the suppressive effects of other shoots in a neighbourhood on a focal shoot of weight w at census t (Yokozawa and Hara, 1992). The $C(t,w)$ function in this paper is defined as the total dry weight of shoots greater than w per 10x10 cm subplot at census t. The absolute growth rate of an individual shoot of dry weight w, Δw, was given as follows according to Yokozawa and Hara (1992):

$$\Delta w = w\,\{a_0 - c_1\, C(t,w) - c_2\, C(t,w_{\min})\}, \qquad (3)$$

where $w_{\min}$ is the minimum shoot weight in the stand, a_0, c_1 and c_2 are constants. The mean of Δw for each w at census t gives $G(t,w)$ [$x=w$ in eqn (1)]. The ratio c_1/c_2 in eqn (3) defines the mode of competition for any size w such that $w_{\min} < w < w_{\max}$ (maximum shoot weight) as follows (Yokozawa and Hara, 1992): if $c_1=0$ and $c_2>0$, competition is two-sided and symmetric, where relative growth rate (RGR) of every shoot is equally suppressed by others (i.e. both larger and smaller shoots) due to stand crowdedness in terms of stand biomass $C(t,w_{\min})$; as c_2 (>0) decreases towards 0 (or c_1/c_2 increases towards infinity) with $c_1>0$, competition becomes more asymmetric (but still two-sided) and completely one-sided (i.e. suppression only by larger shoots) when $c_1>0$ and $c_2=0$ or $c_1/c_2 \to +\infty$ (one-sided competition is an extreme case of asymmetric competition); if $c_1=c_2=0$, competition is absent. Because the average number of shoots per 10x10 cm subplot was less than 2 at censuses 4 and 5 due to high shoot mortality, eqn (3) was applied only to the early growing stages, censuses 1-3, in both the years. The term "$-a_1w^m$" ($a1$ and m are constant parameters) introduced by Yokozawa and Hara (1992) for age effect was omitted in eqn (3). Forward stepwise (independent variables are entered or removed stepwise one at a time) multiple linear regression analysis was conducted for Δw as the dependent variable and w, $wC(t,w)$ and $wC(t,w_{\min})$ as the independent variables. The values of F-statistic to enter and to remove an independent variable were both set at 2. The remaining variation, which was not accounted for by eqn (3), is attributable to the $D(t,w)$ function in eqn (1) where $x=w$. In terms of the regression analysis, the $G(t,x)$ and $D(t,x)$ functions represent the predicted value and variance of residuals, respectively.

The $M(t,w)$ functions for estimated shoot dry weight w in the permanent plots were estimated at each census t in 1991 and 1992 as follows. First, shoot weight was classified into about ten size classes with almost equal intervals so that each size class should contain at least ten shoots. Then, mortality rate (the proportion of dead shoots to the initial number of live shoots) until the next census was calculated for each size class. This value represents the $M(t,w)$ function for w as a mid-point value of each size class at census t.

Results

The R^2 of the allometric relationship described by eqn (2) was generally high in both the years, ranging from 0.774 to 0.971: seven cases out of ten were > 0.9, two cases were

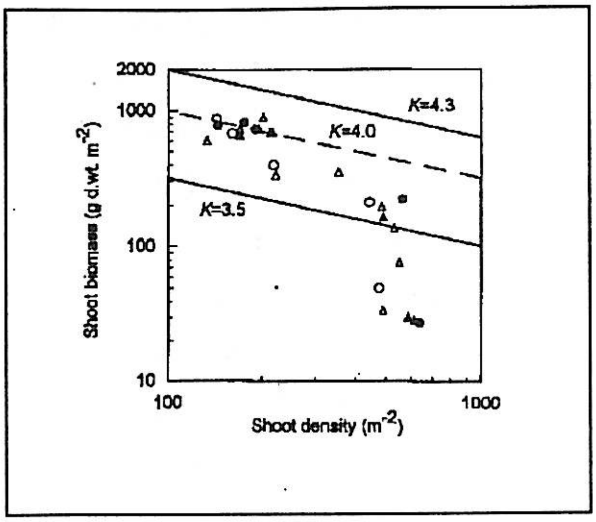

Fig. 1. The relationship between shoot density p (m^{-2}) and shoot biomass y (g d.wt. m^{-2}) of *Urtica dioica* on log-log scale during a growing season in 1991 (Δ,○) and 1992 (▲,●). Triangles represent the sample-number-weighted mean of five 25x100 cm harvested plots, and circles the sample-number-weighted mean of four 1x1 m permanent plots [each shoot weight was estimated using eqn (2)]. The self-thinning line given as $\log_{10}y + (1/2)\log_{10}p = K$ (constant) is presented for $K=3.5$, 4.0 and 4.3.

> 0.8, and one case was 0.774. Shoot emergence occurred until census 2 in both the years: 19 and 86 shoots emerged between census 1 and 2 in 1991 and 1992, respectively.

High mortality of *Urtica dioica* shoots occurred from the beginning of the growing season both in 1991 and 1992 (Figs 1 and 2). The biomass-density relationship of *Urtica*

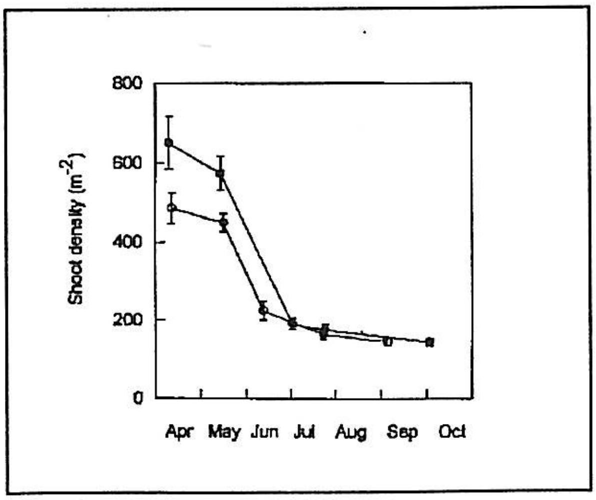

Fig. 2. Changes in shoot density (m^{-2}) of Urtica dioica during a growing season in 1991 (○) and 1992 (●). Each symbol represents the mean of four 1x1 m permanent plots together with SE bars.

dioica shoots fits in a band given by the two self-thinning lines described as $\log_{10}y + (1/2)\log_{10}p = K$ (y, biomass [g d.wt. m-2]; p, density [m^{-2}]; K, constant) with K=3.5 and 4.3 (Fig. 1), which have been reported for many non-clonal self-thinning plants (Yoda et al., 1963; Westoby, 1984; White 1985; Weller 1989). The relationship between shoot density per 10x10 cm subplot at census 1 (X) and the number of dead shoots per subplot between census 1 and 3 (Y) in the four 1x1 m permanent plots in 1991 was: Y=-0.569(±0.117SE)+0.589(±0.018SE)X, n=363 (empty subplots excluded), R=0.863 (linear regression analysis). Shoot mortality rate per subplot given as Y/X was thus positively dependent on shoot density per subplot because the intercept was significantly negative and the slope was significantly positive. The same result was obtained between census 1 and 5 and also for 1992. Although the initial shoot density in April was different between the years, shoot density converged to almost the same value towards the end of the growing season (Fig. 2).

Urtica dioica shoots grew vigorously in shoot height, diameter and weight in a growing season (Figs 3-5). There was little difference in the pattern of size-structure

Table 1. The results of multiple linear regression analysis based on eqn (3) for the shoot weight growth of *Urtica dioica* in 1991 and 1992. All the tagged shoots in 91 10x10 cm subplots randomly selected from the four 1x1 m permanent plots were used for calculation. Because the shoot number per 10x10 cm subplot was not enough at census 4 and 5, regression analysis was not conducted between census 3 and 5. The forward stepwise method was used and the step number each independent variable was entered into the regression is given in parentheses (no variables were removed). The blank means that the variable was not entered. The R^2-values for the final model is d.f.-adjusted. See text ("Materials and methods") for the census dates of each year.

	Year 1991 *P*-value	R^2-value	Year 1992 *P*-value	R^2-value
census 1-2	(n=403)		(n=429)	
a_0	0.000	(1) 0.449	0.000	(1) 0.243
c_1				
c_2	0.008	(2) 0.460		
final model	0.000	0.457	0.000	0.241
census 2-3	(n=198)		(n=171)	
a_0	0.000	(1) 0.367	0.000	(1) 0.543
c_1				
c_2	0.078	(2) 0.377	0.045	(2) 0.554
final model	0.000	0.371	0.000	0.549

Table 2. Mortality and competition patterns of clonal plants in comparison with those of non-clonals in crowded monospecific stands

Plants	density-dependent shoot self-thinning	competition between living shoots
many clonals	none, almost none or only in later growing stages	none, almost none or symmetric
Brachypodium pinnatum$^{1)}$	none	asymmetric
Carex flacca$^{1)}$	almost none	asymmetric
Urtica dioica$^{2)}$	from the early growing stage each year	almost none
Gynerium sagittatum$^{3)}$	occurs over years	asymmetric
non-clonals	**from the early growing stage**	**mostly, asymmetric**

1) from De Kroon and Kwant (1991) and De Kroon, Hara and Kwant (1992); 2) this study; 3) from De Kroon (1993) and De Kroon and Kalliola (1994). For references for "many clonals" and "non-clonals", see text.

dynamics between the two years (Figs 3-5). In accordance with the great decrease in shoot density, size variability in terms of the coefficient of variation (CV) and skewness decreased from the second census onwards in shoot height, diameter and weight (Figs 3-5). Mortality rate of individual shoots, $M(t,w)$, was negatively size-dependent from the beginning of the growing season (Fig. 6). Mortality rates based on shoot height and diameter showed the same results as for shoot weight in Fig. 6. The Kolmogorov-Smirnov two sample and Mann-Whitney *U*-tests revealed that the $C(t,w)$ values at census 2 of shoots that died during census 2 and 3, where shoot mortality was greatest (Fig. 2), were significantly ($P<0.01$) greater than those of living shoots, whilst there was no significant difference ($P>0.1$) in the $C(t,w_{\min})$ values between the living and dying shoots. These results indicate that shoot mortality was caused by asymmetric competition between living and dying shoots. There was little difference in the growth and mortality patterns of shoots between 1991 and 1992.

For the multiple linear regression analysis based on eqn (3), homogeneity of variances of residuals (homoscedasticity) was checked with residual-predicted value scatterplots. Since the residuals had constant variances in all the cases in Table 1 [i.e. the $D(t,w)$ function was size-independent as pointed out by Hara et al (1993) as a common feature of many clonal plants], transformation was not made for Δw. Normality of residuals and outliers were checked with normal plots and residual-deleted residual plots, respectively, and no serious discrepancies were found. The Durbin-Watson statistic was between 1.9 ~ 2.0 and serial correlation between residuals was between -0.1 ~ 0.1 in all the cases in Table 1, implying little autocorrelation between residuals. Therefore, none of these residual analyses indicates inadequacy of the regression model, eqn (3). Multicollinearity was not found between the independent variables in eqn (3) since correlations between $C(t,w)$ and $C(t,w_{\min})$ were all less than 0.5. Symmetric competition between living shoots was detected ($P<0.1$) at census 1-2, 2-3 in 1991 and at census 2-3 in 1992. However, increases in the R^2-values were relatively low (ca. 1 %; Table 1) even when the competition variable, $wC(t,w_{\min})$, was entered. The intercept for eqn (3) was not significantly different from 0 ($P>0.1$) in all the four cases in Table 2.

Discussion

It has been demonstrated extensively that in non-clonal crowded monospecific plant tands (mostly artificial ones) intense density-dependent self-thinning (sensu Yoda t al., 1963), which is brought about by negatively size-dependent mortality, occurs rom the early growing stage and that competition between individuals is suggested to be "asymmetric" (or "one-sided") [reviews by Weiner and Thomas (1986), Hara (1988) and Weiner (1990); note that the precise definition of "asymmetric" (or "one-sided") competition differs amongst authors, but the common view of "asymmetric competition" many authors, including us, have used is the one described verbally by Weiner (1990)]. In clonal plants, however, physiological integration between shoots [Hutchings, 1979; for example, see reviews of Pitelka and Ashmun (1985) and Hutchings and Slade (1988a, b)] brings about the support of smaller shoots (or shoots in the dark) by the transport of resources from larger shoots (or shoots in the light), especially early in the growing season, resulting in the delay or absence of density-dependent shoot self-thinning, little (or symmetric) competition between shoots and the decrease in shoot size variability (for example, Hutchings, 1979, 1983; Bradbury, 1981; Cain, 1990; Hara et al., 1993). These growth and mortality patterns of shoots are brought about also by the utilization of remobilized resources in rhizomes (Bradbury, 1981; Cain, 1990; Hara et al., 1993), which can also

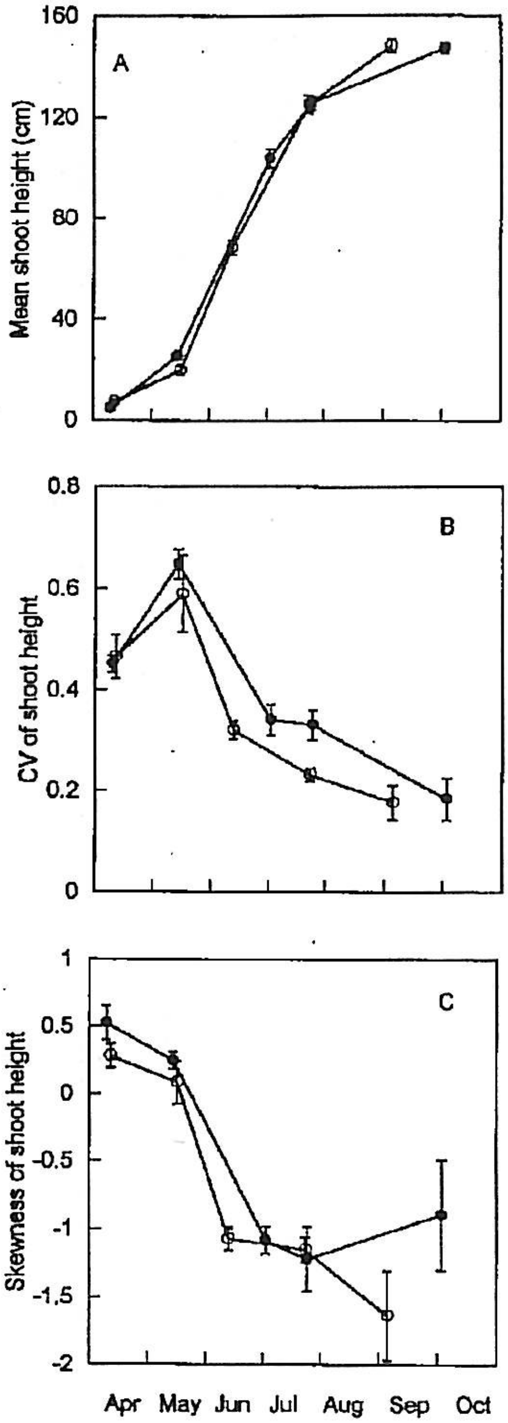

Fig. 3. Changes in mean (A), CV (coefficient of variation) (B) and skewness (C) of shoot height of *Urtica dioica* during a growing season in 1991 (○) and 1992 (●). Each symbol represents the mean of four 1x1 m permanent plots together with SE bars.

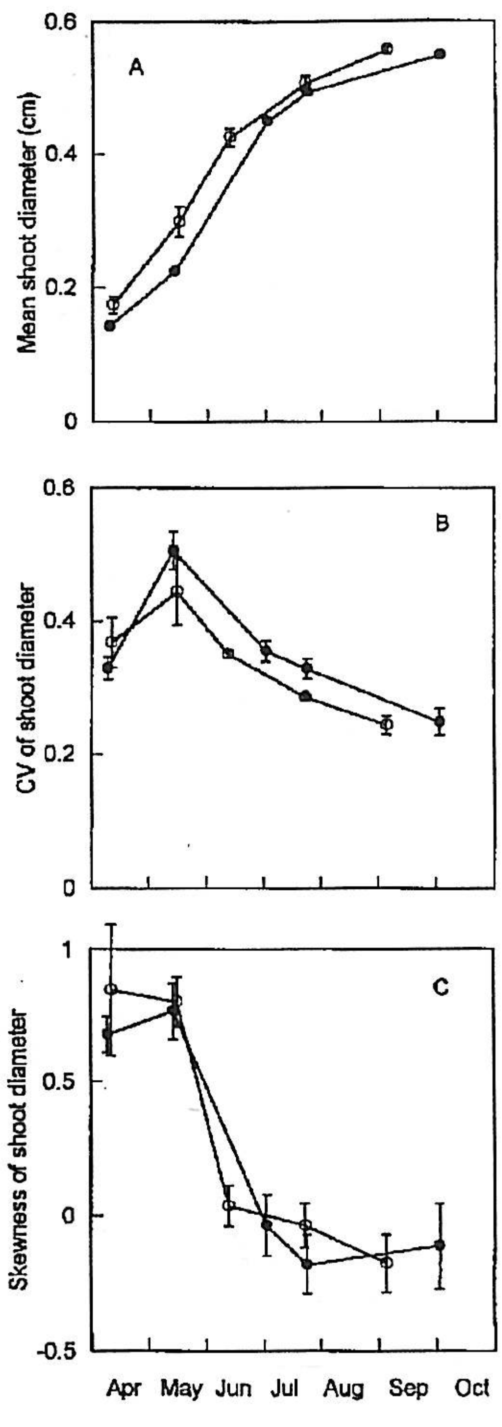

Fig. 4. Changes in mean (A), CV (coefficient of variation) (B) and skewness (C) of shoot diameter at ground level of *Urtica dioica* during a growing season in 1991 (○) and 1992 (●). Each symbol represents the mean of four 1x1 m permanent plots together with SE bars.

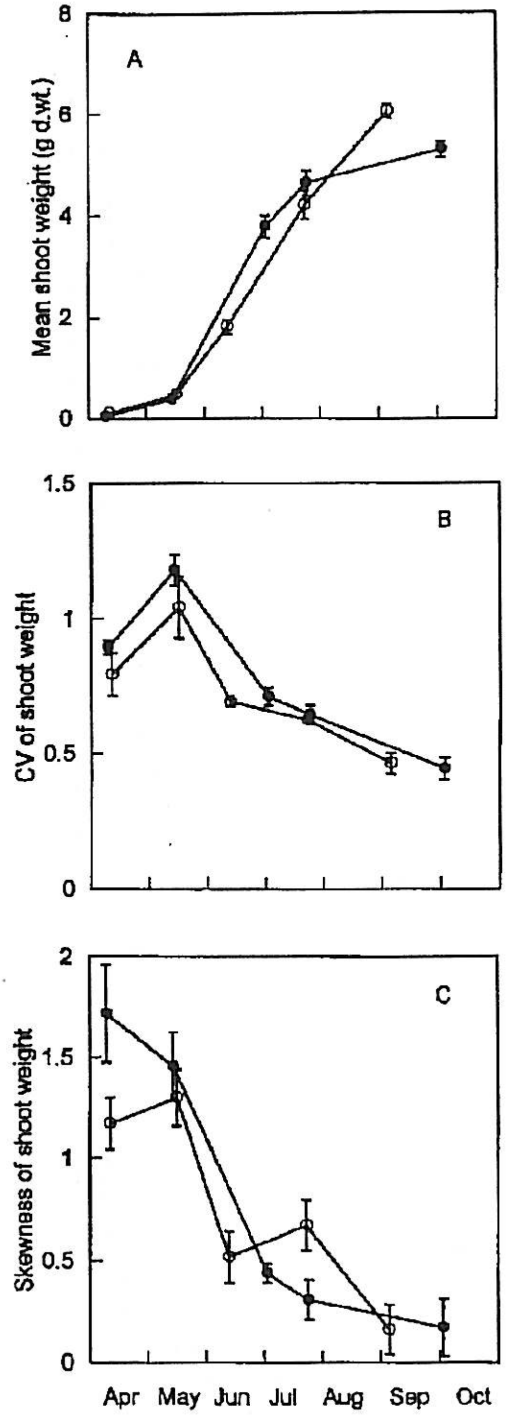

Fig. 5. Changes in mean (A), CV (coefficient of variation) (B) and skewness (C) of estimated shoot weight of *Urtica dioica* during a growing season in 1991 (○) and 1992 (●). Each symbol represents the mean of four 1 x 1 m permanent plots together with SE bars.

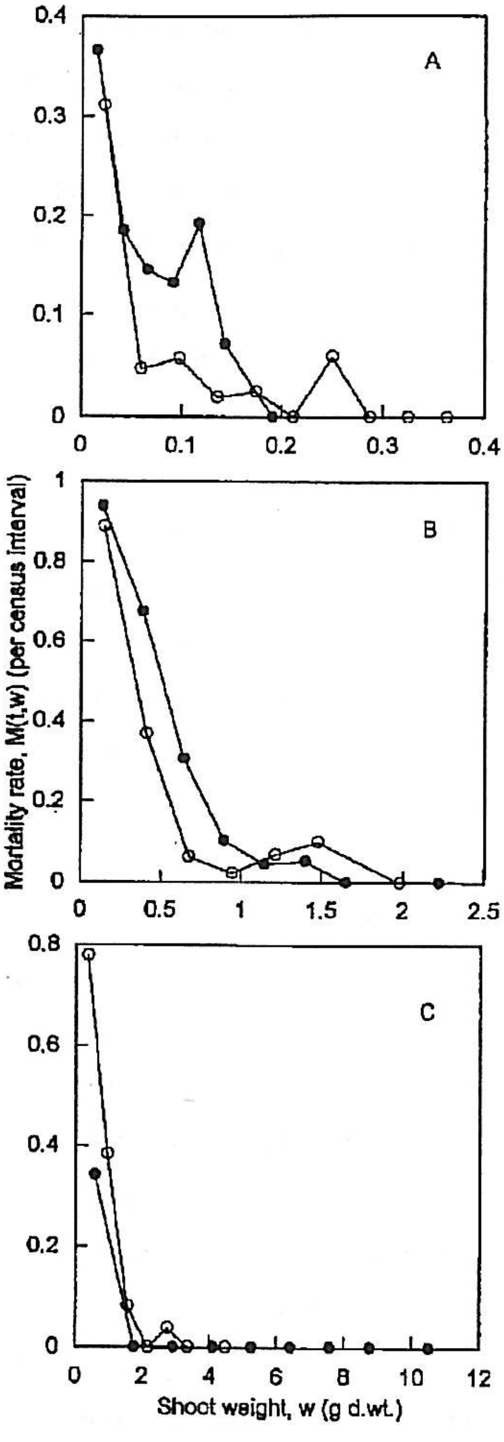

Fig. 6. The *M(t,w)* functions [mortality rate in eqn(1)] of estimated shoot weight of *Urtica dioica* at census 1-2 (A), cencus 2-3 (B) and census 3-4 (C) in 1991 (○) and 1992 (●). All the tagged shoots in 91 10 x 10 cm subplots randomly selected from the four 1 x 1 m permanent plots were used for calculation. See text ("Materials and methods") for the census dates in each year.

be regarded as physiological integration in a broad sense.

Due to physiological integration between shoots, the growth, competition and mortality patterns of clonal plants are supposed to be different from those of non-clonal plants. The degree of physiological integration, however, differs amongst clonal plant species (Kirby, 1980; Bradbury, 1981; Ashmun, Thomas and Pitelka, 1982; Hartnett and Bazzaz, 1983; Noble and Marshall, 1983; Pitelka and Ashmun, 1985; Schmid and Bazzaz, 1987; Magda, Warembourg and Labeyrie, 1988; Tissue and Nobel, 1990; Hutchings and Price, 1993), including the case of absence of physiological integration (De Kroon and Kwant, 1991; De Kroon et al., 1992; De Kroon, 1993). Therefore, the growth, competition and mortality patterns of shoots must also differ amongst clonal plant species (for example, Hara et al., 1993; Hara 1994). In *Brachypodium pinnatum* and *Carex flacca*, shoot competition was inferred to be asymmetric, clone competition was inferred to be symmetric and there was little indication for density-dependent shoot self-thinning (De Kroon and Kwant, 1991; De Kroon et al., 1992). In the clonal forb *Polygonum cuspidatum*, shoot competition was suggested to be symmetric and shoot mortality did not occur (Suzuki, 1994a, b). In *Phragmites australis,* shoot self-thinning was confined only to the later growing stages and little shoot competition was inferred even under crowded conditions (Van der Toorn and Mook, 1982; Hara et al., 1993). In the clonal grass *Festuca rubra*, shoot mortality occurred size-independently during a growing season and shoot competition was suggested to be either symmetric or absent (Hara and Herben, unpublished results). In these studies, the mode of shoot/clone competition was assessed (or inferred) based on shoot/clone weight growth.

Against the hypothesis of physiological integration, De Kroon (1993) and De Kroon and Kalliola (1994) argue that the reason why shoot self-thinning rarely occurs in many clonal plants is that the maximum size the shoot reaches at the final stage in a growing season is relatively small in many clonal species, and hence the duration of shoot self-thinning is relatively short in a growing season of clonal plants (Westoby, 1984). De Kroon (1993) and De Kroon and Kalliola (1994) argue that density-dependent shoot self-thinning must occur if this condition is relaxed as in the clonal giant grass *Gynerium sagittatum,* which grows up to 8-15 m after several years of growth without dying back each year in tropical South America. Their assertion was supported by their harvested data of *Gynerium sagittatum*: shoot density^@stem volume (per unit ground area) relathinship was negative on log-log scale and mean stem volume (per shoot)—Gini coefficient relationship was also negative [but note that De Kroon (1993) and De Kroon and Kalliola (1994) did not follow the time course of shoot self-thinning].

The great decrease in shoot density (survival rate at the end of a growing season was about 30 %), density-dependent shoot self-thinning and negatively size-dependent shoot mortality of *Urtica dioica* were remarkable from the beginning of the growing season in both the years (Figs 1 and 2). It was also shown that shoot mortality of *Urtica dioica* occurred as a consequence of asymmetric competition between living and dying shoots. This type of shoot mortality, i.e. shoot self-thinning as in non-clonal crowded monospecific stands, has not been reported yet for clonal plants except the suggestion by De Kroon (1993) and De Kroon and Kalliola (1994) for *Gynerium sagittatum.* However, it should be noted that intensive shoot self-thinning of *Urtica dioica* occurred in one growing season (from April to October in a year), whilst shoot self-thinning of *Gynerium sagittatum* was suggested to occur over years. *Solidago canadensis* (Bradbury, 1981), *Mercurialis perennis* (Hutchings, 1983) and *Solidago altissima* (Cain, 1990) showed a decrease in shoot density during a growing season. However, the survival rate at the end of the growing season was above 50 % and these authors suggested that the decrease in shoot density was not due to density-dependent self-thinning.

Table 1 indicates that there was no evidence for one-sided or asymmetric competition in the weight growth of living shoots of *Urtica dioica.* Moreover, the degree of detected symmetric shoot competition was very low, because increases in the R^2-values were almost negligible (ca. 1 %; Table 1) when the symmetric competition variable, $wC(t,w^{\min})$, was entered into the regression. In conclusion, competition between living shoots of *Urtica dioica* was almost absent, although intense shoot self-thinning was brought about by asymmetric competition between living and dying shoots from the beginning of the growing season. Cain (1990) also suggested that intraclonal competition in *Solidago altissima* was negligible. However, Cain (1990) calculated only correlations between the height of the focal shoot (not growth rate or shoot weight) and that of all the neighbours (thus only symmetric competition was considered). The use of only shoot height for the mode of competition may be misleading (Hara et al., 1991), especially when shoots grow also in diameter as in *Urtica dioica* of this study. The use of a model only for symmetric competition may also be misleading

(Thomas and Weiner, 1989; Hara and Wyszomirski, 1994), because it cannot detect the degree of competitive asymmetry.

The growth, competition and mortality patterns of the clone may be different from those of the shoot (cf. De Kroon et al., 1992). In this study, however, it was impossible to distinguish between clones in the field (for example, which and how many shoots belonged to a single clone and how many clones were in the study plots). If there were many clones in the study plots and clone competition (competition between shoots belonging to different clones) was intense, this must be reflected in the results of Table 1. Table 1, however, gives no evidence for intense clone competition in the field (evidence for any competition was tenuous), suggesting that either (1) there were only a few clones or (2) many clones in the study plots rarely competed. The former case (1) is most likely because forbs as *Urtica dioica* are considered to show asymmetric intense competition if the stand is crowded with many clones (Hara, 1986; Hara and Yokozawa, 1994).

In summary, intensive density-dependent shoot self-thinning, which was brought about by asymmetric competition between living and dying shoots, occurred in *Urtica dioica* as in non-clonal crowded monospecific stands (but not as in most clonal plants), but competition between living shoots was almost absent as in many clonal plants (but not as in many crowded non-clonal plants). Therefore, the growth and mortality patterns of *Urtica dioica* shoots are conspicuous in comparison with other clonal plants. These shoot dynamics of *Urtica dioica* form a new pattern not reported yet for clonal plants. The mortality pattern of *Urtica dioica* is as that of non-clonal crowded plants, but the growth and competition pattern of living shoots is as that of clonal plants. The former may be explained by the "maximum shoot size" hypothesis of De Kroon (1993) and De Kroon and Kalliola (1994); the latter may be a result of physiological integration as in many clonal plants (resources of dying shoots may also be absorbed by living shoots in a single clone). Otherwise, there may simply be a control of shoot-size-dependent physiological integration that smaller shoots most likely to die are not supported by larger growing shoots and the sharing of resources occurs only amongst growing shoots. There must be a wide spectrum of the growth, competition and mortality patterns of shoots of clonal plants. *Urtica dioica* is in between the two extremes of the generally accepted "clonal" and "non-clonal" plants (Table 2). It should be important to recognize the growth, competition and mortality patterns in this spectrum for the study of life-history evolution of clonal plants.

Acknowledgements

We thank Tomáš Herben and Hans de Kroon for valuable discussions and comments on the manuscript. This study was supported by a grant for international collaboration from the Japan Society for the Promotion of Science.

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chapter 6

VERTICAL DISTRIBUTION OF UNDERGROUND ORGANS OF *PHALARIS ARUNDINACEA* L. AND *URTICA DIOICA* L. IN A FLOODPLAIN: COMPARISON OF TWO METHODS

Vertikální distribuce podzemních orgánů *Phalaris arundinacea* a *Urtica dioica* v říční nivě: srovnání dvou metod

Vertical distribution of underground organs of *Phalaris arundinacea* and *Urtica dioica* in a floodplain: a comparison of two methods

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Preslia, v tisku

Klimešová J. et Šrůtek M. (199.): Vertical distribution of underground organs of *Phalaris arundinacea* and *Urtica dioica* in a floodplain: a comparison of two methods. - Preslia, Praha, 00:000-000.

Keywords: Floodplain, method of soil monolits, rhizomes, profile wall method, roots

Vertical distribution of underground organs was studied in monospecific stands of *Urtica dioica* and *Phalaris arundinacea* and in mixed stand of the two species in the floodplain of the Lužnice River (South Bohemia, Czech Republic). The method of soil monolits and the profile wall method were used; both gave the same results for root distribution in deeper soil horizonts. Roots of both species were found in the whole soil profile down to the groundwater table. By the method of soil monolits, the rhizomes of *P. arundinacea* were found deeper than by the profile wall method. Both methods revealed a higher concentration of roots in the topsoil in the stand of *U. dioica* stand than in that of *P. arundinacea*. In the shallowest soil layer, fewer roots were found by the profile wall method than by the method of soil monolits, probably because the finest roots were not recorded by the former. The profile wall method was less time-consuming and less demanding for special equipment than the method of soil monolits.

Úvod

Podzemní orgány rostlin nejsou rozloženy v půdním profilu rovnoměrně, až 80 % kořenové biomasy je soustředěno ve svrchních 10 cm půdy (Fiala 1987). Aktuální distribuce kořenů je modifikována mnoha faktory, z nichž kolísání hladiny podzemní vody je určující pro vertikální distribuci kořenů druhů odolných i citlivých k zaplavení rostoucích v mokřadech (Jackson et Drew 1984).

U. dioica a *P. arundinacea* mají odlišnou vnímavost k nedostatku kyslíku v půdě. Zaplavený kořenový systém *U. dioica* přestává růst a odumírá; nové kořeny rostou pouze na ponořených částech nadzemních výhonů. *P. arundinacea* ve stejných podmínkách pokračuje v růstu (Klimešová 1994a). V nivě řeky Lužnice v Jižních Čechách se však *U. dioica* šíří v suchých letech do porostů *P. arundinacea* a lze zde nalést mozaiku čistých i smíšených porostů obou druhů. Z uvedeného lze soudit, že každý z druhů má jinou vertikální distribuci podzemních orgánů vzhledem k hloubce půdy, tj. vzrůstajícímu nebezpečí zaplavení.

Výzkum rozložení podzemních orgánů rostlin postihne - v závislosti na použité metodě - vždy jen některý z aspektů distribuce podzemních orgánů (Böhm 1979, Schuurman et Goedewaagen 1965). Hluboké půdy bez skeletu a jedno- či dvou-druhový porost na zkoumané ploše nám umožnily, pro svou podobnost s polními kulturami, využít dvou metod nejčastěji používaných v zemědělském výzkumu. Jsou to:
(1) metoda monolitů. Standardní, nejčastěji doporučovaná i používaná metoda (Böhm 1979, Fiala 1987). Principem metody je odběr sloupců půdy o malém oběmu speciálním vrtákem, extrakce kořenů a přepočítání jejich hmotnosti na větší objem půdy;
(2) metoda půdního profilu. Metoda spočívá v zákresu kořenů přeseknutých stěnou půdní sondy (Jeník 1954) a lze ji kvantifikovat (Böhm 1979, Schuurman et Goedewaagen 1965).

Cílem studia byla odpověď na tyto otázky:

a) Liší se porost *U. dioica*, *P. arundinacea* a smíšený porost obou druhů rozložením kořenů a oddenků v půdním profilu?

b) Dávají požité metody studia vertikální distribuce podzemních orgánů rostlin stejné výsledky?

c) Která metoda je pro daný účel studia výhodnější?

Materiál a metody

Terénní práce jsme prováděli 11. až 18. srpna (zakreslování kořenových map na půdním profilu) a 20. září 1988 (odběr půdních monolitů ručním vrtákem) v nivě řeky Lužnice nedaleko obce Halámky v Jižních Čechách. Rozložení podzemních orgánů jsme zkoumali v mozaikovitém porostu *P. arundinacea* a *U. dioica* na plochách lišících se pokryvností obou druhů a hloubkou podzemní vody:

Plocha 1 (UD)- porost *U. dioica* (odhadnutá pokryvnost nadzemních výhonů *U. dioica* 95 %, *P. arundinacea* 5 %) měl hloubku hladiny podzemní vody 110 cm. Velikost mapovaného půdního profilu byla 100 x 100 cm a hloubka odběru půdních monolitů 100 cm.

Plocha 2 (UD+PA) - smíšený porost *U. dioica* a *P. arundinacea* (pokryvnost *U. dioica* 50 %, *P. arundinacea* 50 %) měl hladinu podzemní vody v hloubce 100 cm. Velikost mapovaného půdního profilu byla 120 x 100 cm a hloubka odběru půdních monolitů 80 cm.

Plocha 3 (PA) - porost *P. arundinacea* (pokryvnost *P. arundinacea* 100 %) s hladinou podzemní vody v hloubce 70 cm. Velikost mapovaného půdního profilu byla 100 x 70 cm a hloubka odběru půdních monolitů 70 cm. Substrátem byla ve všech případech hlinitopísčitá oglejená nivní půda.

Metoda monolitů

Půdní monolity byly odebrány po 20 cm hloubky ručním vrtákem o průměru 70 mm ve vzdálenosti asi 1 m od stěny půdního profilu, který byl mapován. Vzorky byly promyty na 2 mm sítě; kořeny a oddenky byly ručně přebrány od příměsí, usušeny při 90 °C a zváženy. Rozlišili jsme pouze oddenky obou druhů, kořeny se nám odlišit nepodařilo (popis metody viz Fiala 1987). V hloubce větší než 60 cm byly vzorky ze všech opakování sloučeny pro malé množství kořenů a soubory nebyly proto mezi sebou statisticky porovnávány.

Metoda půdního profilu

Na zkoumaných plochách byla ručně vykopána půdní sonda až k hladině podzemní vody. Jedna stěna byla zarovnána a pomocí provázku a hřebíků na ni byla udělána síť 10 x 10 cm. Každé pole sítě bylo vidličkou zbaveno asi 0.5 cm vrstvy zeminy a současně byly takto odhalené kořeny a oddenky mapovány na milimetrový papír při zachování pozice a délky segmentů. Oddenky a kořeny obou druhů se nepodařilo rozlišit. Současně byly zakresleny základní vlastnosti půdního profilu. Výsledná mapa byla rozdělena na obdélníky 10 cm (šířka) x 20 cm (hloubka) a na nich byl spočítán počet kořenů a oddenků přeseknutých půdním profilem (popis metody viz Böhm 1972).

K hodnocení výsledků byla použita jednofaktorová analýza variance a mnohonásobné srovnávání pomocí konfidenčních intervalů (např. Zar 1974).

Výsledky

Oddenky *U. dioica* jsme zaznamenali do hloubky 20 cm, ale oddenky *P. arundinacea* i ve vrstvě půdy z hloubky 40 až 60 cm (tab.1). Kořenů do hloubky ubývalo, ale byly nalezeny až po hladinu spodní vody. Průkazné rozdíly v množství kořenů mezi jednotlivými porosty jsme zaznamenali jen v hloubce 20 až 40 cm, kde měly největší hmotnost kořeny v porostu *P. arundinacea* (tab.1). Množství kořenů ve smíšeném porostu *U. dioica* a *P. arundinacea* bylo stejné jako v porostu *U. dioica*. Největší celkovou hmotnost podzemních orgánů jsme zjistili v porostu *P. arundinacea* (tab.1).

U všech tří porostů jsme metodou půdního profilu zjistili přítomnost oddenků do hloubky 20 cm, přičemž oddenky *U. dioica* a *P. arundinacea* nebyly od sebe ve smíšeném porostu odlišeny. V hloubce asi 40 cm začínal u všech typů porostů půdní horizont nesoucí známky redukčního (bezkyslíkatého) prostředí. Kořenů ubývalo s hloubkou půdy, ale ve všech případech byl prokořeněný celý půdní profil až po současnou hladinu spodní vody. Studované porosty se lišily množstvím kořenů a oddenků do hloubky 40 cm (tab.2). Do hloubky 20 cm bylo nejvíce kořenů i oddenků v porostu *U. dioica* a nejméně ve smíšeném porostu *U. dioica* a *P. arundinacea*. Ve vrstvě půdy z hloubky 20 až 40 cm měl nejvíce kořenů porost *P. arundinacea* a nejméně porost *U. dioica*.

Tab. 1 - Průměrná hmotnost kořenů a oddenků [gm^{-2}] zjištěná metodou monolitů v porostu *Urtica dioica* (UD), *Phalaris arundinacea* (PA) a smíšeného porostu obou druhů (UD+PA). V závorkách jsou uvedeny směrodatné odchylky; průměry na téže řádce označené různými písmeny jsou rozdílné na hladině významnosti 5% - hodnoty pro kořeny a oddenky testovány odděleně (jednorozměrná analýza variance, mnohonásobné srovnávání pomocí konfidenčních intervalů). n - počet opakování; # - vzorky odebírány pouze do hloubky 70 cm; K - kořeny; O - oddenky; - oddenky nebyly nalezeny; + - vzorky ze všech opakování byly sloučeny.

Table 1 - Average dry weight of roots and rhizomes [g.m^{-2}] examined by the method of soil monolits in stands of *Urtica dioica* (UD), *Phalaris arundinacea* (PA) and in their mixed stand (UD+PA) The means bearing the same letter rowwise were not statistically different at $P < 0.05$ - means for roots and rhizomes tested separately (one-way ANOVA, confidence intervals); standard deviations are given in parentheses; n - number of replicates; # - soil profile not deeper than 0.7 m; - rhizomes not found; K - roots; O - rhizomes; + - samples from all replicates were put together.

hloubka P půdy [cm]		UD n=4			UD+PA n=10			PA n=5	
	K	O-PA	O-UD	K	O-PA	O-UD	K	O-PA	O-UD
0-20	341.7^{a} (152.6)	111.8^{A} (214.9)	277.4 (154.8)	429.3^{a} (244.3)	527.3^{AB} (444.1)	258.9 (295.1)	900.7^{a} (441.7)	1267.7^{B} (67.3)	-
20-40	57.2^{a} (13.9)	-	-	47.0^{a} (18.9)	11.2 (10.9)	-	193.4^{b} (92.8)	23.9 (15.1)	-
40-60	25.3^{a} (16.3)	-	-	19.2^{a} (10.4)	8.1^{+}	-	28.6^{a} (24.3)	-	-
60-80	15.6^{+}	-	-	15.1^{+}	-	-	$3.6^{\#+}$	-	-
80-100	4.6^{+}	-	-	-	-	-	-	-	-
celková podzemní biomasa [gm^{-2}]	883.0			1337.8			2417.8		

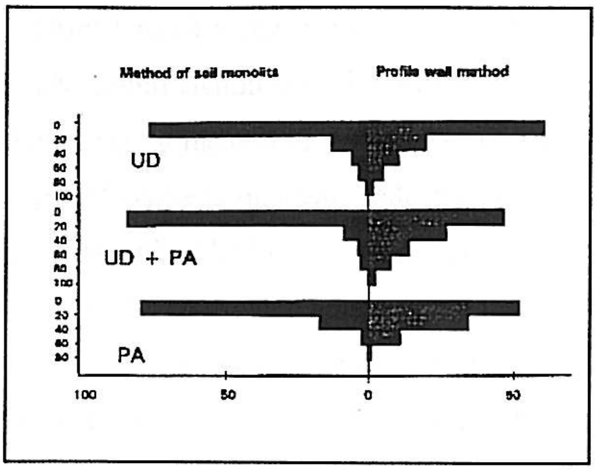
Tab.2 - Průměrný počet kořenů a oddenků přeseknutých půdním profilem v porostu *Urtica dioica* (UD), *Phalaris arundinacea* (PA) a smíšeného porostu obou druhů (UD+PA) na výseku půdního profilu o rozměrech 10 x 20 cm. V závorkách jsou uvedeny směrodatné odchylky; průměry na téže řádce označené různými písmeny jsou rozdílné na hladině významnosti 5% - hodnoty pro kořeny a oddenky testovány odděleně (jednorozměrná analýza variance, mnohonásobné srovnávání pomocí konfidenčních intervalů); n - počet opakování; # - hloubka půdního profilu jen 70 cm; - oddenky nezaznamenány; K - kořeny; O - oddenky.

Table 2 - Average number of root and rhizome segments recorded in 10 x 20 cm fields of a soil-profile wall in stands of *Urtica dioica* (UD), *Phalaris arundinacea* (PA) and in their mixed stand (UD+PA) The means bearing the same letter rowwise were not statistically different at $P < 0.05$ - means for roots and rhizomes tested separately (one-way ANOVA, confidence intervals); standard deviations are given in parentheses; n - number of replicates; # - soil profile not deeper than 0.7 m; - rhizomes not found; K - roots; O - rhizomes.

hloubka půdy [cm]	UD n=10		UD+PA n=12		PA n=10	
	K	O	K	O	K	O
0-20	89.6^{b} (11.9)	18.9^{B} (3.54)	67.6^{a} (14.62)	10.4^{A} (3.92)	74.4^{ab} (17.42)	17.3^{B} (6.04)
20-40	29.9^{a} (6.33)	-	39.1^{ab} (6.32)	-	49.7^{b} (15.99)	-
40-60	15.8^{a} (6.53)	-	20.9^{a} (7.14)	-	16.3^{a} (6.04)	-
60-80	8.5 (3.50)	-	11.5 (7.61)	-	$1.3^{\#}$ (0.82)	$-^{\#}$
80-100	2.9 (2.28)	-	3.9 (2.75)	-	#	#

Metodou monolitů jsme u všech tří porostů zaznamenali ve svrchním horizontu půdy větší akumulace kořenů než metodou půdního profilu (obr.1). Pomocí obou metod jsme nalezli nejvíce kořenů v hloubce 20 až 40 cm v porostu *P. arundinacea.*

Na studium prováděné metodou monolitů bylo zapotřebí 6 pracovních dní dvou pracovníků a speciální vybavení (kořenový vrták, lopatka, metr, igelitové pytlíky, promývací síta, zdroj vody, sušárny, váhy). Metoda půdního profilu si vyžádala čtyři pracovní dny dvou pracovníků a jednoduché vybavení (rýč, lopatka, metr, vidlička, hřebíky, provaz, tužka a milimetrový papír).



Obr. 1 - Vertikální distribuce kořenů [%] po 20 cm hloubky půdy ve třech typech porostů zjištěné metodou půdních monolitů (vlevo) a metodou půdního profilu (vpravo). UD - *Urtica dioica*; UD+PA - smíšený porost *Urtica dioica* a *Phalaris arundinacea*; PA - *Phalaris arundinacea.*

Fig. 1 - Vertical distribution of roots [%] in three types of stands shown for 20 cm horizontal soil layers,. UD - *Urtica dioica*; UD+PA - mixed stand of *Urtica dioica* and *Phalaris arundunacea*; PA - *Phalaris arundinacea.* The results obtained by the method of soil monolits are compared with those provided by the profile wall method.

Diskuse

Použitými metodami studia vertikální distribuce podzemních orgánů rostlin jsme u obou druhů zaznamenali prokořenění celého půdního profilu až po současnou hladinu podzemní vody. Toto zjištění souvisí s tím, že od poslední dubnové záplavy do doby našeho výzkumu v srpnu a září roku 1988 nedošlo k významějšímu kolísání hladiny podzemní vody, ani zaplavení, protože byly průtoky vody v řece Lužnici nízké (Klimešová 1994b).

Oběma metodami jsme zjistili stejné rozdíly v množství kořenů mezi zkoumanými porosty ve všech vrstvách půdy kromě 0 až 20 cm. Zatímco pomocí metody půdního profilu bylo zjištěno při povrchu půdy nejvíce kořenů v porostu *U. dioica*, metodou monolitů nebyly díky velké variabilitě a malému počtu opakování nalezeny v této vrstvě statisticky průkazné rozdíly. Podobně Fiala (Fiala 1973, 1976) uvádí korelaci mezi počtem rhizomů přeseknutých půdním profilem a jejich biomasou až v hloubce 30 až 70 cm.

Metodou půdního profilu jsme zjistili ve svrchním horizontu půdy menší akumulace kořenů ve srovnání s horizonty hlubšími než metodou monolitů. Důvodem by mohlo být přehlédnutí nejjemnějších kořínků, které mohly být navzájem slepeny (cf. Böhm et al.

1977) nebo různý směr růstu kořenů v různé hloubce (u vertikálně rostoucích kořenů je menší pravděpodobnost přeseknutí stěnou půdního profilu).

Rozdílné výsledky poskytly metody při hodnocení vertikální distribuce oddenků v půdě: metodou půdního profilu jsme zaznamenali oddenky jen ve svrchních 20 cm půdy, ale metodou monolitů jsme nalezli oddenky *P. arundinacea* ještě v hloubce kolem 50 cm. Padání oddenků do půdní sondy při odběru půdních monolitů je považováno za běžné úskalí metody (Schuurman et Goedewaagen 1965). Přes pozornost, kterou jsme věnovali odběru nemůžeme vyloučit, že odběrový vrták vmáčkl oddenky do hlubších vrstev vlhké, hlinitopísčité nivní půdy. Při malé hustotě oddenků a různém směru jejich růstu můžeme však očekávat větší pravděpodobnost zachycení jejich výskytu metodou monolitů, která není závislá na směru růstu podzemních orgánů.

Vertikální distribuce kořenů ve smíšeném porostu *U. dioica* a *P. arundinacea* zjišťovaná metodou monolitů se podobala vertikální distribuci porostu *U. dioica*, avšak byla-li zjišťovaná metodou půdního profilu bylo rozložení kořenů podobné porostu *P. arundinacea* nebo intermedielní. Ve smíšeném porostu byly nalezeny metodou monolitů oddenky lesknice hlouběji než v porostu *P. arundinacea*, ale vzhledem k hladině podzemní vody, která byla ve smíšeném porostu ve větší hloubce, není rozdíl významný.

Závěr

1) Druhy *U. dioica* i *P. arundinacea* kořenily v celém půdním profilu až po současnou hladinu podzemní vody bez ohledu na oglejení půdy, ale kořeny *U. dioica* byly soustředěny do svrchních horizontů půdy více než kořeny *P. arundinacea*. Oddenky *P. arundinacea* byly rovněž zaznamenány ve větší hloubce než oddenky *U. dioica*. *U. dioica* se tak vyhne zaplavení kořenového systému při mírném kolísání hladiny podzemní vody.
2) Oběma použitými metodami se nám podařilo nalézt stejné rozdíly ve vertikální distribuci podzemních orgánů *P. arundinacea* a *U. dioica* v nivě řeky Lužnice v hlubších vrstvách půdy. Smíšený porost se však podobal vždy více jednomu z jednodruhových porostů v závislosti na použité metodě.
3) Každá z metod má svoje úskalí: při zjišťování vertikální distribuce podzemních orgánů metodou monolitů může dojít k padání či vmačkávání oddenků nebo větších

kořenů do hlubších vrstev půdy při odebírání vzorků; metoda je náročná na čas i technické vybavení. Výhodou naopak je snadnější determinace oddenků různých druhů a nezávislost na směru růstu podzemního orgánu. Metoda půdního profilu naopak podhodnocuje množství jemných, mnohdy slepených kořenů ve svrchních horizontech půdy a nepřesné výsledky lze očekávat u druhů jejichž kořeny rostou v různé hloubce různým směrem; touto metodou se nám nepodařilo rozlišit oddenky obou druhů ve smíšeném porostu. Výhodou této metody je, že lze při mapování kořenů současně sledovat také makroskopické vlastnosti půdy. Především pro svou nenáročnost na čas a technické vybavení je metoda půdního profilu vhodná pro rozsáhlejší studie jednodruhových porostů robustních rostlin s ne příliš jemnými kořeny.

Poděkování

Dr. J. Květovi a L. Klimešovi jsme zavázáni za pročtení textu a opravu angličtiny a dvěma anonymním recenzentům za cenné připomínky.

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