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Review of biology and ecology of *Urtica dioica*

Přehled biologie a ekologie *Urtica dioica*

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Main aspects of biology and ecology of a clonal herb *Urtica dioica* are presented as a review of literature, including the both authors' previous work on the species. Taxonomical position and distribution of the species are described as well as its habitat requirements and the role it plays in plant communities. Mineral nutrition, litter fall and its decomposition, phenology, floral ecology, seed ecology and dispersal, architecture of the root and rhizome system, response to cutting, herbivores feeding on the plant and its competitive ability in relation to other species are also considered.

Keywords: Biology, ecology, review of literature, *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 countries 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 & Bradbury 1986, Grime et al. 1989, Hendry & 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 appeared 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 & Fries 1986; Fig. 1) 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, N and S America; e. g., Hashimoto 1982).

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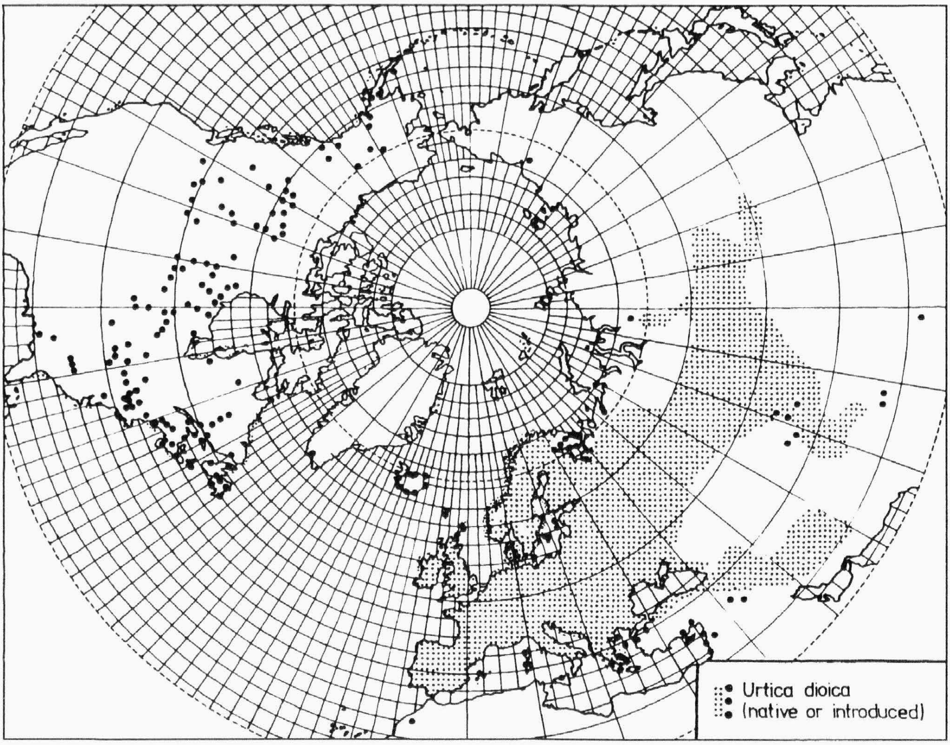

Fig. 1. – Distribution of *Urtica dioica* (Hultén & Fries 1986, adapted)

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

Taxonomy

The chromosome number 2n = 52 was found in Czech populations of *Urtica*[1] (Měsíček & 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, colour, shape and size of leaves; Domin 1944, Geltman 1986, Chrtek 1988) and probably containing a number of subspecies (Ball 1964). Numerous intraspecific taxa have been described but their taxonomical value appears to be disputable (Hegi 1957). Pollard & 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 & 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.

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[1] Nomenclature: Rothmaler W., Schubert R. & Vent W. (1990): Exkursionsflora von Deutschland. Band 4. Kritischer Band. – Volk und Wissen Verlag, Berlin, 812 pp.; Moravec J. et al. (1995): Rostlinná společenstva České republiky a jejich ohrožení. – Severočes. Přír., Příloha 1995 (1): 1–206.

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 (Kravcova 1993).

Phytosociology and species richness

In Central Europe, vegetation with *Urtica* has been a frequent subject of traditional Braun-Blanquetian classification (Braun-Blanquet & Tüxen 1943, Klika 1955, Passarge 1967, Kopecký 1969, Dierschke 1974, Hadač 1984, Messner 1985, Klotz & 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 of 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 *Alnion incanae* Pawł. in Pawł., Sokoł. et Wallisch 1928 (alder and ash 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 & Hejný 1992).

Example for widespread distribution of communities with *Urtica* is the Lužnice River floodplain where 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 floodplain. 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

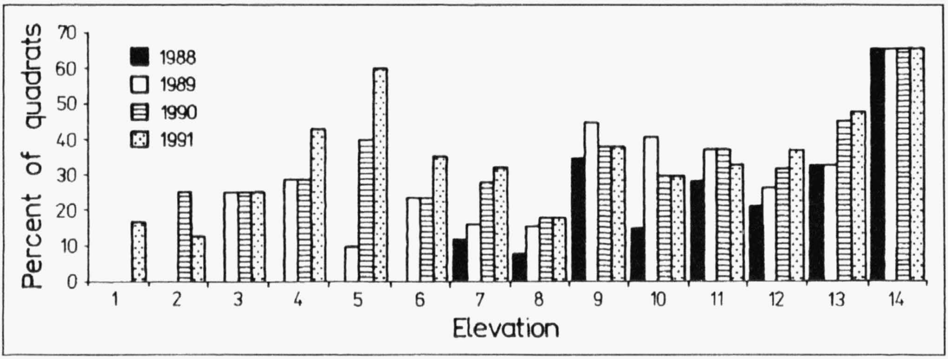

Fig. 2. – Frequency distribution of mature plants of *Urtica dioica* along the gradient of grounwater table (=elevation). Elevation ranges between 455.4 (labelled by 1) and 456.7 m a.s.l. (14) (from Klimešová & Čížková 1996, slightly adapted).

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 in wet meadows lead to a sharp increase of nitrophilous grassy vegetation with ruderal species such as *Cirsium arvense, Urtica dioica, Stellaria media,* and *Anthriscus sylvestris.*

Šrůtek (1997) found that with the water table coming closer to the soil surface, *Urtica* biomass was lower, transpiration decreased remarkably, the plants were shorter, produced fewer branches and rhizomes, and the rhizomes were shorter.

The effects of climatic conditions related to water table depth on distribution and spread of *Urtica* were documented by Klimešová & Čížková (1996). *Urtica* expanded dramatically during three-year drought along observed elevation gradient (Fig. 2).

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 & 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".

Again, the Lužnice River floodplain can be an example for dramatical spread of *Urtica* stand during several last decades. The original occurrence of *Urtica* was probably restricted to river banks in this area. 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 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 & Taylor (1964) suggested that *Urtica* is limited by the concentration of phosphate in the soil and not by nitrogen content (e. g. in the topsoil of woodlands, Pigott 1971). 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 & 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 (Abeyakoon & Pigott 1975). Similarly, 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. Also 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 reached 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 other hand, Teckelmann (1987) found more than 20-fold higher biomass of *Urtica* on a dry ruderalized meadow than on a moist and slightly shaded floodplain site. 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

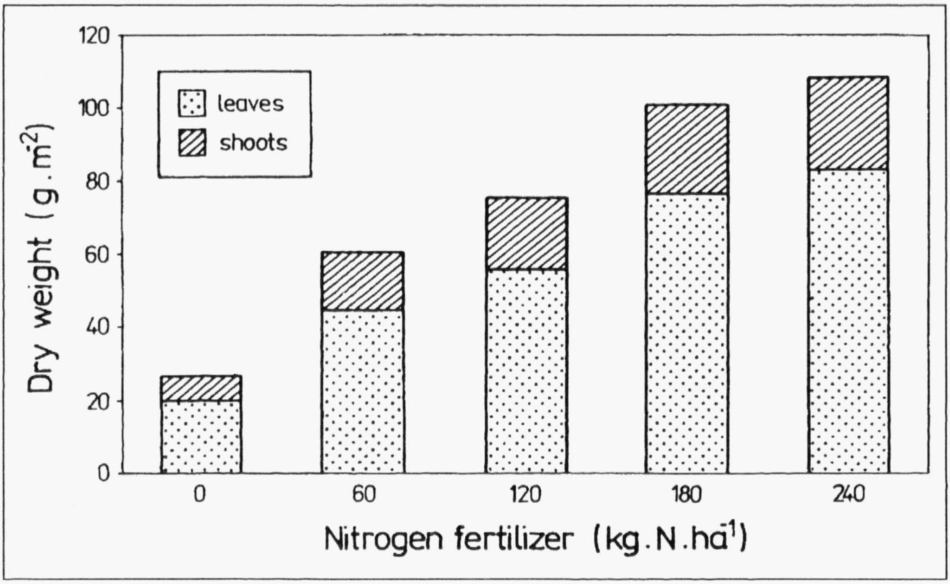

Fig. 3. – Leaf and shoot yield (g.m^{-2}; mean value of both days of harvest) of *Urtica dioica* in dependence on addition of nitrogen-fertilizer (in kg of N per hectare) (from Weiss 1993, adapted).

activity in that part of the plant which exported the reduced nitrogen, i. e. the root in *Plantago lanceolata* and shoot in *Urtica dioica*.

Weiss (1993) documented that increasing amounts of nitrogen always increased herb yield and single-plant yield (Fig. 3). The biomass allocation in *Urtica* plants was significantly affected by nutrient supply in an experiment of Šrůtek (1995), e. g. higher nutrient doses resulted in less biomass allocation to below-ground organs while the period of intensive production of above-ground biomass was prolonged. Branching of the main shoot (number of lateral branches) was positively correlated with plant height and changed with time in his experiment.

The high nutrient supply was shown to shift assimilate partitioning toward producing more leaves 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 & Chapin III 1987, Fig. 4).

Weiss (1993) gave also the analysis of nitrogen in particular organs of *Urtica*. While stems contained 1.8 % total nitrogen, more than twice as much nitrogen was found in the leaves, amounting to 3.7 %. The opposite was true concerning nitrate nitrogen, which reached 2.5 mg nitrate-N.g^{-1}dry matter in the stems, whereas the leaves contained only 0.4 mg.

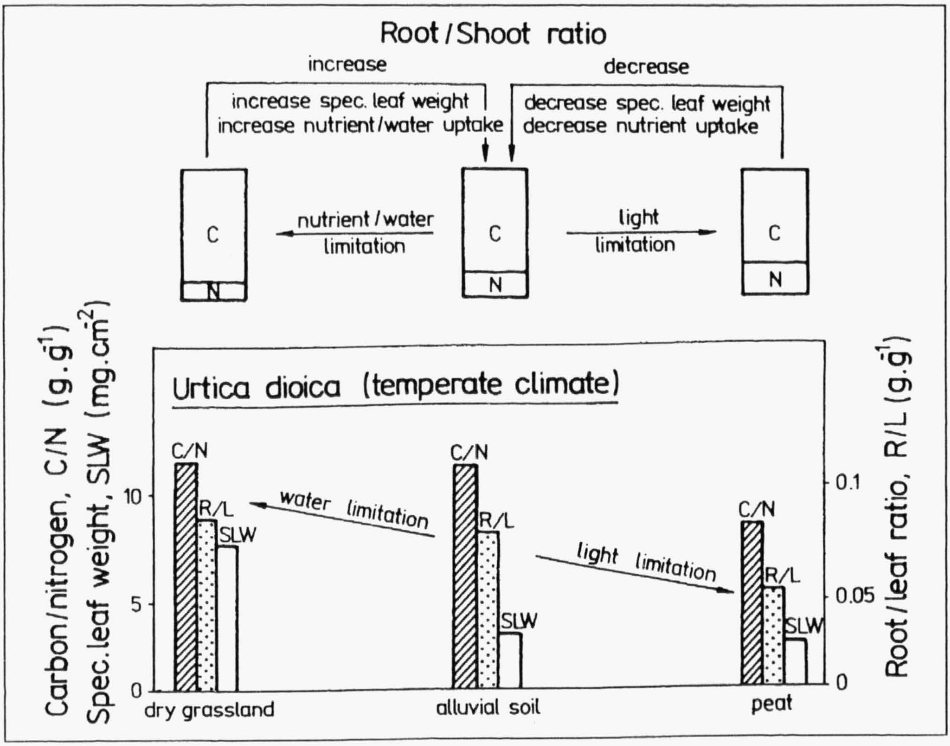

Fig. 4. – Scheme of regulatory plant responses to light, water and nutrient limitations leading to a balanced resource supply (top part). Change of the carbon/nitrogen ratio (C/N), root weight/leaf weight ratio (R/L), and specific leaf weight (SLW) in *Urtica dioica* in Bayreuth, Germany (from Schulze & Chapin III 1987, adapted).

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 below-ground 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 in 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 & Hipkin 1984).

The allometric relations are also affected by nutrient supply and fluctuation of groundwater table (Šrůtek 1995, 1997).

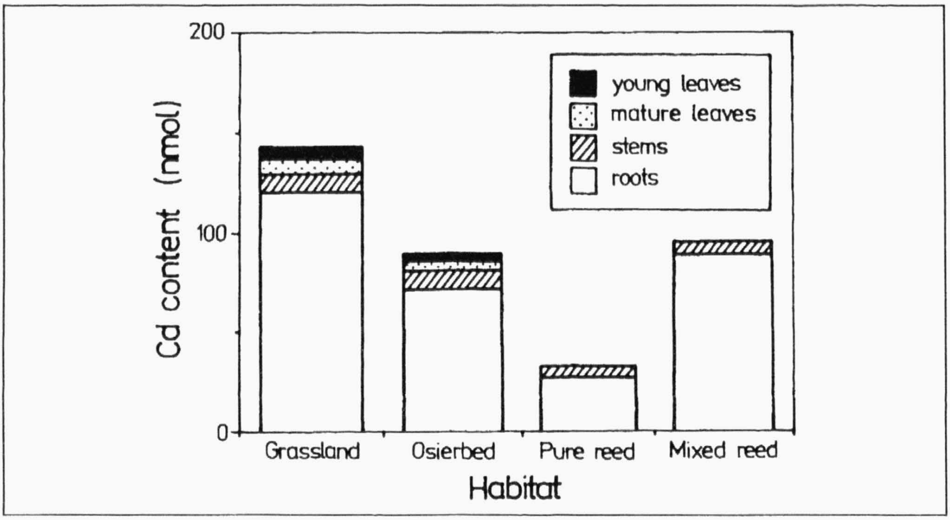

Fig. 5. – Mean cadmium content (i. e. biomass × heavy metal concentration) in plant parts of *Urtica dioica* in pots in different habitats (from Otte & Wijte 1993, adapted).

Urtica is able to accumulate heavy metals in plant tissues. For example, Otte & 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 (Fig. 5).

Litter fall and decomposition

Urtica dioica produces a big volume of litter. Particularly, the stem litter is relatively persistent (Al-Mufti et al. 1977). 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. The speed of decomposition correlated with concentration of aminosugars (Zucker & Zech 1987). Zucker (1987) stressed that the site affects the time course of decomposition, but not the qualitative changes of the sulphur fractions of decomposing *Urtica* leaves.

Processes connected with decomposition have relations to the occurrence of fungi on the growing plants, as well as on the plant litter. As Bell (1974) reported in her review, experimental studies on fungi isolated from *Heracleum sphondylium* and *Urtica dioica* showed that all the primary saprophytic fungi could utilize cellulose, but some species present in the secondary microflora could not do so, and would presumably be consigned to the group of secondary sugar fungi. The primary saprophytes isolated from *Urtica* senescing leaves and adjoining stalk segments are in summer: *Alternaria tenuis, Cladosporium herbarum, Epicoccum nigrum* and *Botrytis cinerea.* The secondary microflora developed in the first winter after litter fall (e. g. *Alternaria tenuis, Cephalosporium* and *Hormiscium* spp.).

Phenology

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. Some of them are killed by frost (Al-Mufti et al. 1977). 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). On a ruderalized dry meadow, Teckelmann (1987) found an initial shoot density of 1800 per sqm in April, decreasing to 270 per sqm in summer, which makes a loss of 85 %.

New rhizomes are produced mainly in late summer or autumn (Greig-Smith 1948).

The peak in biomass production occurs at the end of July (Al-Mufti et al. 1977). Flowering 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 dioecious plant. 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 × 1.0 mm in size and 0.19 mg in weight (Chrtek 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 (Kravcova 1993). As Weiss (1993) found, the prolongation of the growth period increased leaf and stem yield but at the same time leads to a very high number of inflorescences.

Šrůtek (1995) studied effect of various nutrient supply on allometry of plant organs and found that plants grown with higher nutrient addition are not only taller, but at the same height, they have higher inflorescence biomass.

Seed ecology, seedling establishment and vegetative propagation

Only a limited information is available on seed production in *Urtica*. To our 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 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 & 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 (Odum 1978). In the greenhouse, the seeds may germinate after 10 year storage (Bassett et al. 1977). In contrary, Roberts & Boddrell (1984) found the seeds of *Urtica* in cultivated soil being relatively short-lived, and 3 % of seeds 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 van der 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, occurring thus mainly on open and disturbed ground. The sites with dense vegetation cover are unfavourable for the regeneration 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 in the United Kingdom, 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. 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).

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.

Rosnitschek-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 limiting and shading from the surrounding vegetation was too high (Wheeler 1981). The results of Roberts & Boddrell (1984) supported the oppinion of 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 rhizomatous polycarpic perennial, with a hemicryptophyte life form (Chrtek 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).

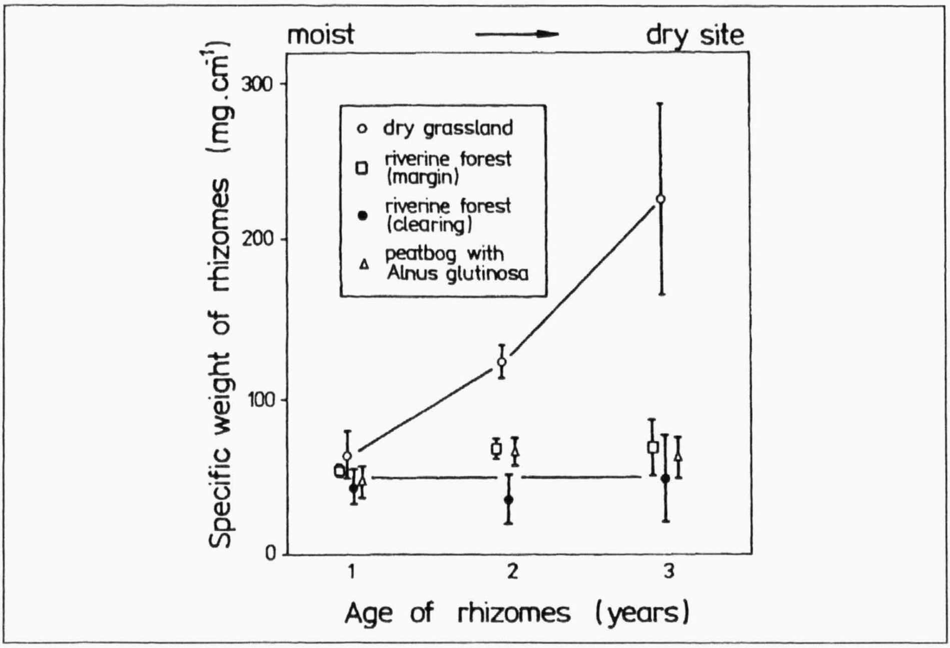

Fig. 6. – Specific weight of *Urtica* rhizomes (dry weight related to rhizome length) in different habitats (studied sites) (from Teckelmann 1987, adapted).

New rhizomes (reddish in colour) are produced 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 branch profusely and form numerous laterals. Older rhizomes and roots are covered with yellow cork layer (Greig-Smith 1948). Roots usually lack mycorrhizas (Grime et al. 1989).

Rhizomes occur usually not deeper than 20 cm under the soil surface (Klimešová & Šrůtek 1995). The architecture of the rhizome system may change under conditions of water storage (Teckelmann 1987): on a dry grassland site old rhizomes of *Urtica* form thick, lignified stems which ensure water supply and distribution during water stress. Under these conditions, all rhizomes show a distinctive secondary growth which is not be the case on sites with abundant water supply (Fig. 6).

Competitive ability

Grime et al. (1989) designated *Urtica dioica* as a strong competitor. Schmidt (1981, 1986) investigated competitive relationships in replacement experiments with *Solidago canadensis* and *Urtica dioica*. Whereas both species grew better in monocultures 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 outcompete *Urtica* totally. Prach & Wade (1992) characterized *Urtica* as a species with highest expansion ability in comparison with other expansive plants, such

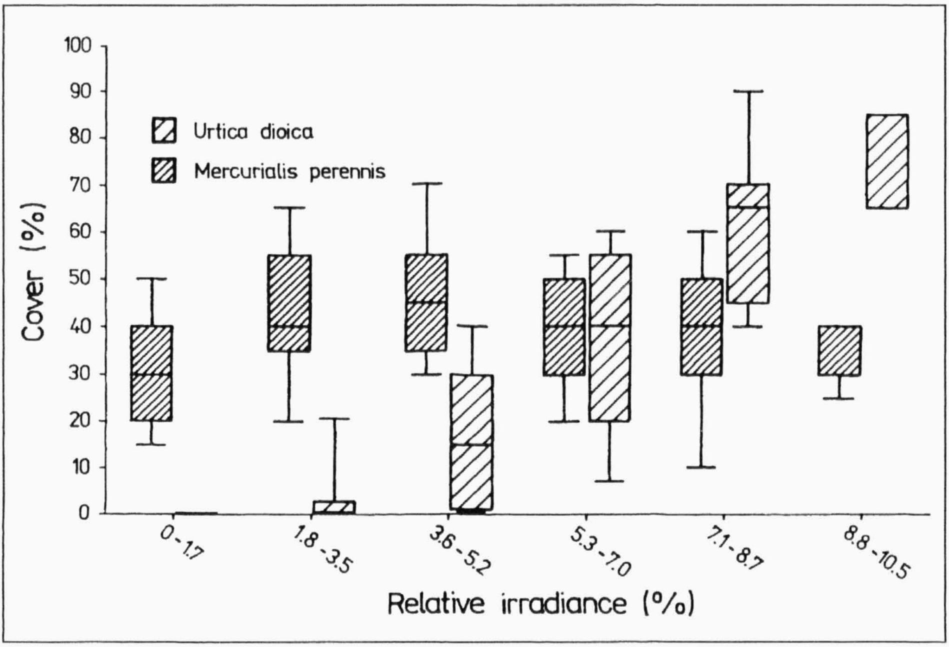

Fig. 7. – Dependence of the cover of *Urtica dioica* and *Mercurialis perennis* on relative irradiance above herb-layer vegetation in 196 10 × 10 m squares in 1995. (Mrotzek et al. 1996, adapted).

as *Agropyron repens, Artemisia vulgaris, Phalaris arundinacea, Calamagrostis epigeios, Epilobium angustifolium, Cirsium arvense, Typha angustifolia* and *T. latifolia*.

Hara & 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). Moreover, 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). Mrotzek et al. (1996) confirmed a linear relationship between growth of *Urtica* and irradiance level. They compared occurrence of two herb species in a beech forest, *Mercurialis perennis* and *Urtica. Mercurialis* was dominant in areas where the relative irradiance was between 3–5 %, above 5 % it is suppressed by the increasing competition from *Urtica* (Fig. 7). Soil chemical properties had only little effect on the species distribution.

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 & Chapin III 1987). The physical support, resembling *Urtica* stems, affects performance and mortality of *Galium*, especially at the highest density (Puntieri & Pyšek 1993).

Growth characteristics related to light conditions

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 & 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 adaptation 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 of *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.

	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 & Palmer 1988).

On the other hand, different interval of cutting affects yield of particular organs. Weiss (1993) found that longer cutting intervals caused a continuous increase in leaf yield. However, the prolongation of cutting intervals leads to a considerable augmentation of flowering and fruiting inflorescences, hence causing a low quality of the herb.

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 & Lersten 1969). Fresh and old leaves were, however, found palatable for some snails (Grime et al. 1968, Grime & Blythe 1969) because it contains no condensed tannins (Lofty 1974). Mason (1974) reported in his review that the stems of *Urtica* proved attractive to snails and this attractiveness occur before actual physical contact, suggesting that plant odours may be important attractants.

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 & 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 better consumption of significant amounts of plant matter. The variation in the number of stinging hairs has a genetic basis.

Pullin & Gilbert (1989) found that the grazing pressure lead 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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Souhrn

Přehled biologie a ekologie kopřivy dvoudomé (*Urtica dioica* L.) uvedený v článku je souhrnem většiny základních literárních prací zabývajících se studiem tohoto druhu. V práci je probráno taxonomické postavení, rozšíření, stanovištní nároky a uplatnění kopřivy ve společenstvech. Další kapitoly jsou věnovány minerální výživě, dynamice živin v pletivech, rychlosti rozkladu odumřelé biomasy, fenologii, tvorbě květů a plodů. Je pojednána také architektura kořenového a oddenkového systému, kompetiční schopnost ve vztahu k jiným druhům, reakce na kosení a dostupné poznatky o herbivorech. Uvedené kapitoly odpovídají stavu poznání v rámci jednotlivých témat.

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