Phenology of *Rumex longifolius*: a key factor for the success of an invasive species?

Fenologie Rumex longifolius: klíčový faktor úspěchu invazního druhu?

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A phenological comparison of *Rumex longifolius* and *R. obtusifolius* was carried out in the Krkonoše mountains at three different altitudes. *Rumex longifolius* proved to be better adapted to the mountain environment, because of its rapid development during the short growth period, and its fast resource allocation into reproductive organs. These features may be one of the reasons for its rapid spread at higher altitudes in Central Europe.

K e y w o r d s : *Rumex longifolius, R. obtusifolius*, allocation of resources, phenology, invasive species, mountain environment

Introduction

Biological invasions and invasive species, as well as the expansion of native species, have become issues of growing interest to many scientists during the last decades (Brock et al. 1997, Carey et al. 1996, Prach & Wade 1992, Pyšek et al. 1995a etc.)

However, most of the so called "invasive species" are expanding only within new territories, while they do not attract any attention in the areas of their origin. Estimating the "invading potential" of a species before an invasion actually takes place is a very difficult task (e. g. Pyšek 1995b). Which features of an invading species make their invasions successful? Which features make them more successful than the native species? This problem has been discussed by many authors (di Castri 1990, Pyšek et al. 1995b etc.).

In some cases, an invasive species is closely related to some native species. In spite of this, it differs considerably in behaviour, e. g. *Heracleum mantegazzianum* (process of invasion in the Czech Republic was described by Pyšek 1991), *Impatiens parviflora* (Trepl 1984) and many others. This is also the case of *Rumex longifolius*, a species alien to the Czech Republic. The species is closely related to several in higher altitudes non–expanding species, such as *R. obtusifolius*, *R. crispus* and others. *Rumex longifolius* is native to northern Europe. It has spread intensively during the last decades not only in Europe, where it has been documented from Scandinavia, Iceland, Russia, the Baltic countries, Great Britain, France, Germany, Spain, Czech Republic and Poland (Jasiewicz 1964, Neumann & Polatschek 1974, Jalas & Lindholm 1975, Kubát 1984, Adler 1992, Tutin 1993, Procházka 1997), but also in South America (Perez-Moreau & Crespo 1972), Canada and Alaska (Neumann & Polatschek 1974).

In the Czech Republic, the first individuals of this species were found in 1961 (Kubát 1984). Since then, it has spread into many new regions and the number of individuals in existing localities has also increased. The history of the invasion within the Czech Republic, particularly in the Krkonoše mountains, has been documented (Kubátová 1994, Kubínová & Krahulec 1997) and the invaded plant communities have also been described.

In Central Europe, the distribution of *R. longifolius* is limited mainly to mountain areas, it does not occur at lower altitudes. This pattern of distribution is probably caused by specific characteristics of the species.

To examine the key features facilitating the invasion, research was undertaken to compare it with a closely related species -R. *obtusifolius*. It is a species with a similar geographical distribution and anatomy; like *R. longifolius*, it grows in a variety of man-made and seminatural habitats, reaches high altitudes, forms individuals of approximately the same size, with simple root systems, and spreads by seed. Of the other related species, *R. crispus* rarely penetrates into mountain regions and requires more ruderal sites. *Rumex alpinus* occurs and spreads in the mountains, but creates polycormons and spreads both by seed and by clonal growth.

For these reasons, *R. obtusifolius* has been selected as the closest species for comparative analysis. The two species are compared not because competition between them would be expected, but merely to help point out features facilitating successful and rapid expansion of one of the closely related species.

Material and methods

Species compared

Rumex longifolius DC. (syn. *R. domesticus* Hartm.) is up to 180 cm tall. Leaves are 20-30 (-40) cm long and 8-10 (-15) cm broad. Valves are approximately 4-5 (-7) × 5-7 mm; tubercles are absent or on one valve only and smaller than 1 mm; achenes are 2.5-3 mm long, brown (Kubát 1990).

Rumex obtusifolius L. is up to 50–100 (–150) cm tall. Leaves are 15–30 cm long and 8–15 cm broad, cordate at the base. Valves are 2.5–6 mm long and 1.5–4 mm broad; tubercles differ in size and occur on one or on all three valves; achenes are 2.5–3 mm long, brown (Kubát 1990). Of the four subspecies only *R. obtusifolius* subsp. *transiens* was present in the localities under study. It is widespread in the Krkonoše mountains, as well as *R. obtusifolius* subsp. *sylvestris. R. obtusifolius* subsp. *subalpinus* has been also documented from the area (Kubát 1990).

Study area

Field work was carried out in three localities in the Krkonoše mountains. The localities were selected because both species under examination were abundant within the sites which made it possible to carry out phenological observations of many individuals from each locality. The localities differ in altitude, but are close to each other, so that it was possible to collect phenological data from all three sites within a day.

The lowest situated site was ca. 1000 m above sea level. It was located on margins of an eroded meadow between the Severka and Bramberk settlements near the town of Pec pod

Sněžkou (50°41'30"N, 15°43'E). The second site (ca. 1200 m a. s. l.) was located in the meadow Liščí louka around the mountain chalet Lyžařská bouda (50°41'N, 15°42'E) on the south-east slope of Liščí hora mountain. The last site was situated at the summit of the mountain Černá hora (50°39'09"N, 15°44'22"E) at the altitude of 1300 m (in fact 1295–1299 m), where the species under study grew along meadow margins, along roads and on ruderal sites.

The growth period begins at approximately the same time at all three altitudes, because the lowest site faces north. Snow melts at the beginning of May. The first frosts occur in November, in cold years even as early as the end of August. Diagrams characterizing the climate of the studied area were published by Krahulec et al. (1997: 11).

Study of phenology

The populations of *R. longifolius* and *R. obtusifolius* were studied during the years 1990–1993.

Biomass production and plant behaviour is influenced by annual climatic variation. Compared with the average temperature and rainfall in the area, the three years may be characterised as follows (Anonymus 1990–1993):

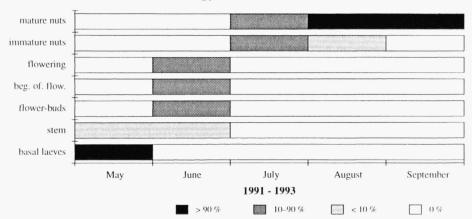
The year 1990 started with a warm and dry spring but otherwise had an average growth period. The year 1991 was very cold with rainfall slightly below average, while 1992 had average temperatures and little rainfall. In 1993, a warm spring was followed by a slightly cooler June with low precipitation; August and September were unusually cold.

The data for both species at all three localities were collected at least once a month during the growth periods, e. g. from April to September. The percentage of individuals in each phenological stadium was estimated for both species. The phenological phases of the two species were described as follows:

- b a s a 1 l e a v e s : only the leaves are developed,
- stem: stem with developing inflorescence growing from the rosette of the basal leaves, but flower-buds are not yet fully developed,
- flower-buds: the inflorescence is fully developed but there are no open flowers,
- beginning of flowering: the buds are fully developed, some of those located in the lower part of the inflorescence begin to flower,
- flowering: most of the flowers of the inflorescence are in bloom,
- i m m a t u r e a c h e n e s : female flowers have turned into achenes, while some male flowers are still flowering,
- mature achenes: most fruits have ripened.

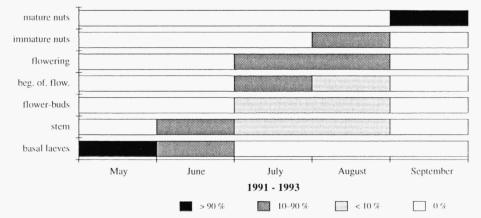
Allocation of resources

The aboveground biomass of 5–15 plants (depending on the population size) of *R. longifolius* and *R. obtusifolius* was collected from the site on Liščí hora mountain (1200 m) four times during the year 1993. The year had a very warm spring (April, May) with low precipitation and a humid and relatively cold July (Anonymus 1990–1993). The temperature increased in the middle of August and reached values above the 50 year average, but late summer was very cold and in some localities the first frosts occurred between August 23–29. In September, there were frosts in many places and temperatures stayed well below average (except the week between September 20–26, which was slightly above average).

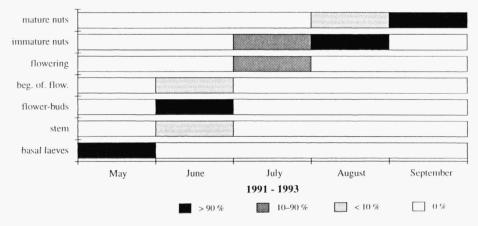


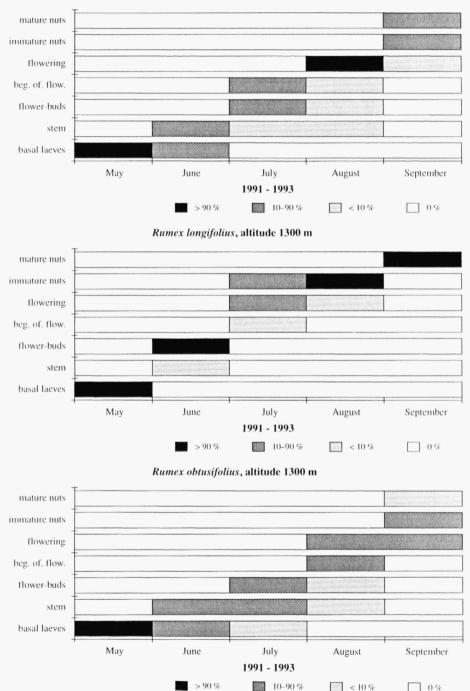
Rumex longifolius, altitude 1000 m





Rumex longifolius, altitude 1200 m





Rumex obtusifolius, altitude 1200 m

Fig. 1. - Phenology of *Rumex longifolius* and *R. obtusifolius* at three different altitudes in the Krkonoše mountains.

The samples of aboveground biomass were sorted into dispersal units (achene together with valves), stems and leaves, dried and weighed. Because the achenes were required for further use for germination experiments the samples were dried up at room temperature. However, the difference in dry mass between these and the samples dried at 80 °C was only a matter of some tenths of grams (maximum 4 % of the dry mass of a sample).

Results

Phenological study

Considerable differences in phenology between *R. longifolius* and *R. obtusifolius* were found in all three sites studied. The results are summarized in Fig. 1.

Both species at all sites developed only sterile basal leaves until the end of May.

In June, the differences in the development of the two species within a site, as well as the differences caused by altitude, became obvious. About 50 % of plants of *R. obtusifolius* developed a stem, while the other 50 % remained in the phase of basal leaves. At the same time, the plants of *R. longifolius* had fully developed flower-buds and many plants were flowering at the lowest altitude (1000 m). Almost no plants of *R. longifolius* at any altitude remained at the phase of sterile basal leaves.

In July, the differences in the development of the two species became even more profound. The plants of *R. longifolius* were flowering, many individuals had already developed achenes and at the altitude of 1000 m, a considerable proportion of them had reached maturity. At the same time, the plants of *R. obtusifolius* were flowering or beginning to flower; at 1300 m a. s. l., they were still in the phase of flower-buds, inflorescence and basal leaves.

The majority of individuals of *R. longifolius* at 1000 m above sea level reached maturity during August, and almost all plants of this species at all altitudes became mature by the end of September.

On the other hand, the first mature individuals of *R. obtusifolius* at 1000 m did not occur until September. Not all plants reached maturity at the higher altitudes and less than 10 % of plants produced mature achenes at 1300 m a. s. l.

Resource allocation

The changes in resource allocation of the two species during the year 1993 at 1200 m above sea level are summarized in Fig. 2.

The dry-mass of fruits of *R. longifolius* constituted more than one third of the total aboveground biomass (38.8 %) as early as August, reaching 53.1 % in September. The decrease in dry-mass during October was caused by dropping achenes, which had been mature since the middle of August.

R. obtusifolius produced an enormous photosynthetic apparatus. Leaves and stems together constituted 87.8 % of the total aboveground biomass in September (19.5 % leaves and 65.9 % stems). Translocation of resources did not occur until October, when the dry-mass of fruits reached 36.8 % with leaves and stems decreasing to 15.7 % and 47.5 % respectively.

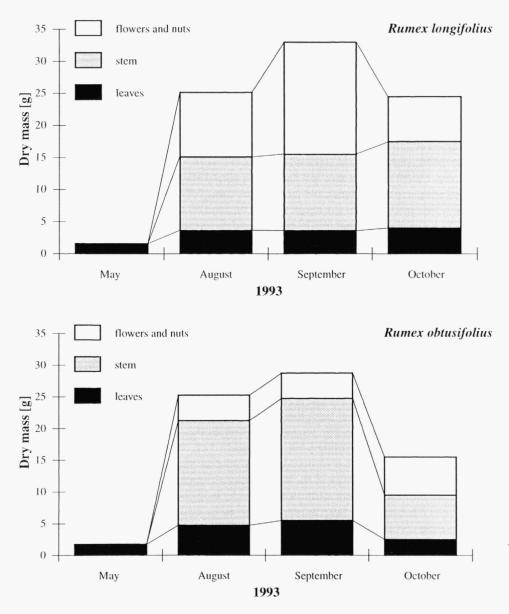


Fig. 2. – Changes in biomass allocation in *Rumex longifolius* and *R. obtusifolius* at 1200 m (the Liščí hora locality).

The differences in resource allocation of the two species under study were analysed by Student's t-test and proved to be significant (P < 0.01) for the period between May and September, while they were not significant in October (P > 0.05).

Discussion

The length of the growth period plays an important role particularly if there are also temperature or moisture limitations.

R. obtusifolius is widespread in Europe, with its northern limit of distribution running through Scandinavia. Although the species is better adapted to lower altitudes, it also penetrates into the mountain regions of the Czech Republic. In the Krkonoše mountains, at the upper limit of its distribution, *R. obtusifolius* develops its photosynthesizing apparatus in summer, when temperature, light intensity and day length are sufficient. The species was studied in the year 1993, which provided optimal conditions for its fast development. The spring was exceptionally warm and the growth period started early. However, because of late flowering due to low June–July temperatures, most of the individuals did not produce mature fruits. In cold years the species could be even less successful. This phenomenon has been described by Grime (1979) for *Reynoutria japonica* in Great Britain.

In the case of *R. longifolius*, the adaptation to areas with a short growth period and temperature limitation is obvious. The species is native to Scandinavia, where, as in the Krkonoše mountains, the number of days in a year with the average temperature exceeding 10 °C is between 90 and 120 (Walter & Lieth 1967). *Rumex longifolius* does not require more than 3–4 months to produce ripe achenes with a very high germination rate (up to 95 % – Kubátová 1994) which enables rapid invasion of the species over short distances and an increase in the number of individuals at the sites.

However, the mechanism of long-distance invasion still remains uncertain. *R. longifolius* represents a rather exceptional case of invasion in the Czech Republic, as it has established itself and spread mainly at higher altitudes.

Most of the invasive species first spread within warmer regions and subsequently penetrate into the mountain areas. *Imperatoria ostruthium*, *Myrrhis odorata* and *Archangelica officinalis* (all of them originally mountain species) are the only neophytes which occurred first at higher elevations (submontane to montane belt, 400–1100 m above sea level). A similar pattern of invasion to that of *R. longifolius* has been described for *Veronica filiformis* (Jehlík 1961, 1998) and *Heracleum mantegazzianum* (Pyšek 1991, 1994). However, unlike the other species mentioned above, *R. longifolius* has never been planted on purpose and it has probably been introduced into the mountain regions unintentionally. No other invasive species is as successful as *R. longifolius* at and above the treeline.

In the future, the spread of this species into lower altitudes is to be expected, as it has already been found on some localities situated at lower altitudes (Kubínová & Krahulec 1997). In general, it will be facilitated by flood waters and river courses, which also played a role in the initial phase of the invasion of *H. mantegazzianum* (Pyšek 1994, Pyšek & Prach 1994).

Summary

The results presented in this study provide a comparison of two closely related dock species: *Rumex longifolius*, invasive at higher altitudes, and *R. obtusifolius* which is less successful at the same altitude. The species were studied in the Krkonoše mountains, where *R. longifolius* spreads extensively, while *R. obtusifolius* occurs only in a few sites and is not abundant there. *R. obtusifolius* may be considered a successful expansive species only at lower altitudes.

R. longifolius uses the few months of the growth period effectively. Mature achenes develop as early as three or four months after the first leaves appear in the spring. From the very beginning of the growth period, considerable amounts of resources are allocated to the reproductive organs. These features enable all individuals, at all the altitudes under study, to produce mature achenes even in cold years.

R. obtusifolius shows the optimum of its distribution at lower altitudes with a longer growth period. Translocation of resources into reproductive organs occurs in late summer, usually in September. Even then, fruits constitute a smaller proportion of the total biomass than in *R. longifolius*. Finally, only a small proportion of individuals of *R. obtusifolius* growing in high altitudes produce mature achenes, especially in cold years.

R. longifolius is a species native to northern Europe, so it is adapted better than *R. obtusifolius* to the short growth period and low temperatures of the mountain environment.

The features of *R. longifolius* described may be one of the key factors influencing the rapid invasion of this species not only in the Krkonoše mountains, but also in other mountain regions of the Czech Republic and whole Central Europe.

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Shrnutí

Studie předkládá výsledky srovnání fenologie dvou blízce příbuzných druhů štovíků – ve vyšších nadmořských výškách rychle se šířícího druhu *Rumex longifolius* a méně úspěšného *R. obtusifolius*. Druhy byly studovány v Krkonoších, kde se *R. longifolius* šíří, zatímco *R. obtusifolius* dosahuje horní hranice svého rozšíření a zůstává omezen především na nejbližší okolí chat.

Fenologie byla sledována v letech 1990–1993 ve třech nadmořských výškách: 1000, 1200 and 1300 m n. m. *R. longifolius* využívá efektivně krátkou vegetační sezónu. Nažky dozrávají již po 3–4 měsících od vyrašení prvních listů. Již od počátku sezóny představuje květenství značnou část celkové biomasy. Všechny rostliny dozrávají ve všech nadmořských výškách, a to i během chladných let.

R. obtusifolius má optimum svého rozšíření v nižších nadmořských výškách s dlouhou vegetační sezónou. Přesun biomasy do generativních orgánů nastává až koncem léta, obvykle v září, ale i pak představují plody menší část celkové biomasy než u druhu *R. longifolius*. Proto ve vyšších nadmořských výškách dozrává jen malá část rostlin *R. obtusifolius*, obzvláště během chladnějších let. V této době bývá růst ukončen prvními mrazy.

R. longifolius je původem ze severní Evropy a je proto lépe než *R. obtusifolius* přizpůsoben krátké vegetační sezóně a nízkým teplotám horského prostředí.

Popsané vlastnosti *R. longifolius* mohou být jedním z klíčových faktorů, který umožnil rychlou invazi druhu nejen v Krkonoších, ale i v jiných horských oblastech České republiky a střední Evropy. S velkou pravděpodobností lze do budoucnosti očekávat invazi druhu i do nižších nadmořských výšek.

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