



Biological Flora of Central Europe

Biological flora of Central Europe: *Rumex alpinus* L.Petra Št'astná^a, Leoš Klimeš^b, Jitka Klimešová^{b,*}^a Faculty of Biological Sciences, University of South Bohemia, Branišovská 31, CZ - 370 05 České Budějovice, Czech Republic and Krkonoše National Park Administration, Dobrovského 3, CZ - 54311 Vrchlabí, Czech Republic^b Section of Plant Ecology, Institute of Botany, Academy of Sciences of the Czech Republic, Dukelská 135, CZ - 379 82 Třeboň, Czech Republic

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ABSTRACT

Rumex alpinus L. (Polygonaceae) is a rhizomatous perennial plant inhabiting stream banks, spring areas, nutrient-rich and mesic to wet abandoned pastures and meadows. It is native in the mountains of Central and Southern Europe but its current distribution has been partly affected by its utilisation as a vegetable and a medicinal herb in the past. This article reviews the literature on the taxonomy, morphology, population biology, genetics, chemistry, physiology and ecology of this species.

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Taxonomy and morphology

Taxonomy

Rumex alpinus L., Sp. Pl.: 334. 1753.

Syn.: *Lapathum alpinum* (L.) Lam., Fl. Franç. 3: 7. 1779. – *Acetosa alpina* (L.) Moench, Menth. Pl. 357. 1794. – *Rumex pseudoalpinus* Höfft, Catal. Pl. Kursko: 26. 1826.

The protologue of *R. alpinus* by Linnaeus in 1753 was based on three herbarium specimens, actually belonging to two *Rumex* species different from the species for which the name *R. alpinus* is currently used, and a species of *Persicaria*. This was established by López González (1988, 1990), who used the name *R. pseudoalpinus* Höfft for the plant long known as *R. alpinus*. As this act became a threat to another well-established name (*R. longifolius*), the name *R. alpinus* was proposed for conservation in the sense of its traditional and current usage, which originates from Linnaeus' description of 1759 (Cafferty and Snogerup, 2000). This proposal was accepted by the Committee for Spermatophyta in 2002 (Brummitt, 2002).

Names in other languages: German: Alpen-Ampfer, Mönchsrhabarber; English: Monk's Rhubarb, Alpine dock; French: Rumex des Alpes, Rhubarbe des moines, Rhapsontie des moines; Italian: Rabarbaro alpino; Spanish: ruibarbo de monjes, rapóntico vulgar; Polish: Szczaw alpejski; Czech: Šťovík alpský.

In the traditional taxonomic system the species belongs to the genus *Rumex* L., subgenus *Rumex* (= *Lapathum* (Campd.) Rech. f.), section *Rumex* (= *Simplices* Rech. f.) and subsection *Alpini* Rech. f. The subsection *Alpini* includes perennial plants with horizontal rhizomes, basal leaves broad and cordate at base, valves entire, without tubercles. As subsections of the section *Rumex* Rech. f. reflect phenotypic similarity between species rather than their relatedness (Rechinger, 1949a), some authors suggested to merge the subsections established by Rechinger. For example, Borodina (1979) placed *R. alpinus* into a broader subsect. *Patientiae* Rech. f. A recent phylogenetic study of the genus based on ITS sequences (Navajas-Pérez et al., 2005) demonstrated monophyly of the subgenus *Rumex*. Unfortunately, due to a relatively low number of representatives of the subgenus in that study, detailed evaluation of the relationships between species within the subgenus is not yet possible. The genus *Rumex* belongs to the family *Polygonaceae* Juss. and to the order *Polygonales* Dumort.

Morphology

R. alpinus is a perennial species consisting of a horizontal rhizome, above-ground vegetative shoots with three to five big leaves, and fertile stalks bearing smaller leaves and up to several thousands of flowers and fruits.

Rhizomes

The monopodially branching rhizome (Fig. 1) of dark brown color is formed by a shortened base of a shoot, which is pulled into the soil by contracting roots. The rhizomes grow usually at a depth

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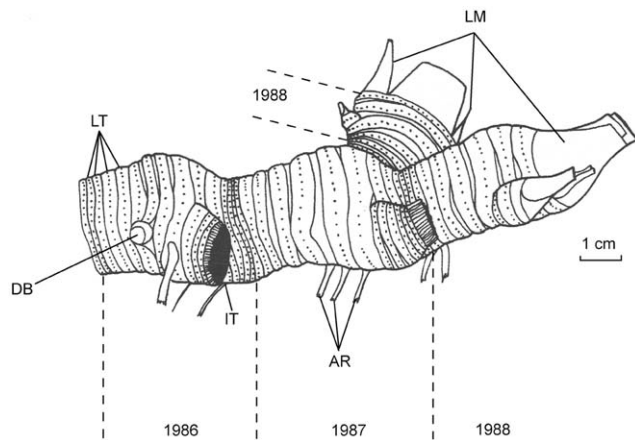


Fig. 1. Terminal part of the monopodial rhizome of *Rumex alpinus*, side view. LM – living meristems beneath leaf bases, LT – leaf scars, IT – inflorescence scars, DB – dormant bud, AR – adventitious roots; numbers refer to the years in which the segments were produced (adapted from Klimeš, 1992).

of up to 5 cm (Klimeš, 1992; Rudyshin and Tsarik, 1982), less frequently 10–12 cm (Kliment, 1988). The mean depth of 30 cm given from the High Tatra Mts. by Šmarda (1963) seems to be erroneous, as *R. alpinus* hardly regenerates if buried to depths below 20 cm (Klimeš et al., 1993; see also section “Response to abiotic factors”). The apical bud grows endlessly producing leaves, unless damaged, lateral branches are vegetative or flowering.

The rhizomes are evenly segmented and their cross-section is of deep-orange color, oval, flattened in the horizontal plane. Each segment is a product of one growing season, corresponding to annual increments (Šmarda, 1963; Klimeš, 1992) therefore, the actual age of individual rhizome branches can easily be estimated. However, total age of an individual plant can be determined only in plants that originated from seeds, in which is the oldest part of rhizome with primary main root still preserved.

The widest part of the segments develops in the middle of the growing season (summer), whereas constricted parts are formed in spring and autumn (Šmarda, 1963). The length of rhizome segments is about 4 cm; the width is 2–3 cm (Klimeš, 1992). On each rhizome segment up to six large lateral buds are formed, but only one to two produce leaves in the current year. Next year they either become dormant or continue their growth and form rhizome branches or form a flowering shoot (Klimeš, 1992). If the apical meristem of a rhizome is damaged, one or several resting lateral buds, usually the youngest ones situated closely to the former apical meristem, are activated (Klimeš, 1992).

The rhizome branches usually from the second year of plant life, more intensively when plant is growing on margin than inside of closed stands of *R. alpinus* (Klimeš, 1992). Branches arise at about right angles (Šmarda, 1963; Klimeš, 1992). If the rhizome is branched, gradual decay of the oldest parts results in fragmentation or the clone into physically independent ramets, clonal fragments (Klimeš, 1992).

Rhizome segments are transversely stripped by leaf scars (Fig. 1). As the petiole base clasps the rhizome, the leaf scars with remnants of vascular bundles are preserved all around the rhizome segments, forming well-visible rings. These leaf scars are the widest at the thickest part of the rhizome segment and narrower towards segment constrictions. One segment bears amount of scars corresponding to the number of leaves produced per year. Remnants of leaf bases are usually preserved for several weeks to months (Šmarda, 1963). The distance between subsequent leaf scars corresponds to internode length, and usually varies from 1 to 2 mm. If rhizomes are buried or cross each other,

their internodes may elongate to several centimetres (Klimeš et al., 1993). Scars indicating the previous position of flowering and fruiting shoots are preserved laterally during the entire life-span of the rhizome. The information “stored” on rhizome may be used for retrospective plant population studies (e.g. Klimeš, 1992; Št'astná, 2005).

According to data from the Krkonoše Mts., Low Tatra Mts. and Alps, segments persist for 13 years at the average (Klimeš, 1992; Grabherr and Mucina 1993; Št'astná pers. obs.). Exception is record by Šmarda (1963) from the High Tatra Mts. who found mean age of rhizomes only 8 years. Maximum segment persistence observed in the Krkonoše Mts. was 20 years (Klimeš, 1992), in the Low Tatra Mts. at the highest locality in this mountain range (1900 m a.s.l.) 35 years (Št'astná unpublished). Prolonged segment persistence is generally observed at higher elevations. The length of rhizomes depends on rhizome age and site conditions. Šmarda (1963) recorded a mean length of about 45 cm for living rhizomes and nearly 20 cm for preserved dead parts. The length of the 35-year-old rhizome from the Low Tatra Mts. was about 120 cm.

Roots

The primary root (0.15–0.25 mm in diameter) of seedling loses its dominant role in the second year of plant life, but is often preserved for more than 10 years. A bunch of adventitious roots develops in upper third of on rhizome segment of the current year in density 5–6 (7) per 1 cm, at the place of branching up to 15 or more per 1 cm of rhizome length, but only some of them survive to the following year. The adult plant has the roots mostly grown from lateral and bottom parts of a rhizome, roots are about 10 mm in diameter (Kutschera and Lichtenegger, 1992). Total length reported by Rudyshin and Tsarik (1982) is up to 100 cm; according to Kutschera and Lichtenegger (1992) is up to 300 cm. The most of belowground biomass usually reach depth of 20–40 cm (Šmarda, 1963; Kutschera and Lichtenegger, 1992). Width of the root system was 229 cm for the individual from the Karawanken region (Kutschera and Lichtenegger, 1992).

Roots are fleshy, tough, from white-cream (thin and young ones), over yellow-orange, to medium brown and sometimes lightly reddish, stout at the basal part (Kutschera and Lichtenegger, 1992; Kubát, 1990). Young roots serve as major absorbents of nutrients (Esau, 1965; Klimešová and Klimeš, 1996). The lifetime of individual root ends with decaying part of rhizome, thus about 13 years.

Leaves

Basal leaves consist of a petiole of up to 70–80 cm long (Šmarda, 1963) and an undulate lamina which is up to 50 cm long and to 20 cm wide (Hegi et al., 1977). Its apex is rounded, the leaf margin is flat or slightly sinuate, and the base is widely and deeply cordate with rounded basal lobes. Leaves occur also on flowering shoots but there stay alive only during the flowering period and later, during maturing of seeds, they die. These leaves differ in size and shape: leaves from basal part of a flowering shoot are similar to ones produced by apical meristem of a rhizome, leaves from the middle part are smaller and rounded at base and the leaves from upper part are minimized to several cm and cuneiform (Rechinger, 1957; Kubát, 1990; Šmarda, 1963; Rechinger and Akeroyd, 1992). The youngest leaves are convoluted and covered with a mucus, thin transparent to whitish membrane and adherent base of previous leaf. The membrane remains attached to the leaf until it elongates to about 20 cm (Šmarda, 1963) or less, depending on the final size of the leaf. Apical rhizome bud is protected by the leaf bases, axillary resting buds are covered by scale leaves.

Reproductive organs

Flowering shoots arise from last year lateral branches (dicyclic shoots), their apical meristem changes from vegetative to flowering already in autumn (Klimešová, pers. obs.). Usually one or two, exceptionally four, flowering shoots are initiated per rhizome segment. Flowering shoots are robust, leafy, but without a basal rosette, longitudinally ribbed, about 30–200 cm tall, erect, shortly papillose to glabrous (Rechinger, 1957; Hegi et al., 1977; Kubát, 1990; Rechinger and Akeroyd, 1992). The inflorescence is an indeterminate thyrs. It is narrowly spindle-shaped, crowded, bearing small leaves alternately arranged; its branches are fasciculate, repeatedly branched.

Flowers are usually bisexual. However, some plants are polygamous, with male-sterile flowers developed at the base of the inflorescence and female-sterile flowers at the top (Šmarda, 1963). In some inflorescences functionally unisexual flowers may strongly prevail (Pushkarev, 1984) and andromonoecy, gynomonoecy and even dioecy are reported (Klimeš, 1994; Jäger and Werner, 2005). Flowers situated near the base of the inflorescence start to flower first, flowers at the top develop last.

The diameter of flowers range from 4 to 5.5 mm (Aeschimann et al., 2004), petals are greenish and without calus (Hegi et al., 1977; Müller-Schneider, 1986), external perianth is elongated, its base is tightly adjoined to the internal perianth (Rechinger, 1957). Peduncles are filiform, 2–5 times longer than the valves, conspicuously thickened under the valves, and consisting of two segments. Valves (Fig. 2) are cordate to oval, with reticulate venation, broadly acute, 4–6 mm long and 3.5–5 mm wide, entire, without tubercles. Achenes (Fig. 2) are 2.5–3 mm long, dark umber, bright (Rechinger, 1957; Müller-Schneider, 1986; Kubát, 1990; Rechinger and Akeroyd, 1992), their weight is 1.62 mg (Krkonosé Mts., Št'astná, unpublished data).

R. alpinus pollen grains belong into pollen class 3-zono or 2–4 pantocolporate. Colpus of ectoaperture is narrow, long and slit-like, not or only slightly sunken, margins distinct, with acute ends. Endoperture with slightly elongated porus, costae endopori present, sometimes interrupted at the equator, but distinct. Sexine is thicker than nexine, sexine is uniform in thickness, with scabrae on the surface (visible only in scanning electronic microscope). Ornamentation is microreticulate (brochi < 1 µm). Muri is simplicolumellate with scabrae on the surface (visible

only in scanning electronic microscope). Lumina is circular, ellipsoidal to irregular in outline. Equatorial view is ellipsoidal (oblat) to circular, polar view is ellipsoidal to circular. Pollen size is 24.57 ± 1.48 µm polar (P) and 26.50 ± 1.59 µm in equatorial (E) view, P/E ratio: 0.93 ± 0.03 (according to sample from Oberurgel 1997, coll. by B. Walhmüller, Glycerine jelly, measured by K. Werner, Inst. of Botany, Innsbruck).

Variation

In contrast to most other species belonging to the subgenus *Rumex*, *R. alpinus* shows little taxonomically relevant morphological variation (Rechinger, 1957). *R. alpinus* var. *subcalligerus* Boiss. belongs to *R. confertus* Willd. (Rechinger, 1949b).

Distribution and habitat requirements

Geographical distribution

R. alpinus is distributed in high mountains of western, central and eastern Europe, including the Apennines, mountains of the Balkan Peninsula and Caucasus, Armenia and North Anatolia (Fig. 3). In Slovakia it occurs in Krivanská Malá Fatra Mts., Velká Fatra Mts., Nízke Tatry Mts., Západné Tatry Mts., Vysoké Tatry Mts., Oravská Magura Mts., Oravské Beskydy (Babia gura) Mts., Bukovské vrchy Mts. (Kliment and Jarolímek, 1995).

It has been introduced to Great Britain (Scotland, since Middle Ages, from lowlands to 375 m a.s.l.), USA (Vermont and Maine, from lowlands to 1500 m a.s.l.), Canada (New Scotland, since 1921) and to Java (Rechinger, 1957; for distribution maps, see Meusel et al., 1965; Jalas and Suominen, 1979). Isolated introduced populations of *R. alpinus* are reported also from Finland since 1923 (Erkamo, 1984), Sweden (since 1997), Norway (Tromsø, escaped from bot. garden) (Jäger in lit.). *R. alpinus* is not autochthonous in some mountain areas of the Czech Republic (e.g. the Orlické Mts., Krkonosé Mts.), where it was introduced in the second half of the 16th and at the beginning of the 17th century (Kopecký, 1973; Kubát, 1990; but see editor's foot-note in Kwiatkowski, 2003 for a different opinion). Its current distribution is in many regions noticeably congruent with the distribution of past and present settlements. The plant is introduced also in the Vosges Mts., in the western part of Central France, in Thuringia and perhaps in the Black Forest.

It is most abundant in montane, subalpine and alpine zones (Rechinger, 1957; Landolt, 1977; Ellenberg, 1988; Ellenberg et al., 1992; Pott, 1996; Aeschimann et al., 2004), from altitude of 800 to about 2600 m (the Bernina Alps: to 2640 m), whereas around streams it descends to 600 m (Rechinger, 1957). Localities with the lowest elevations (apart from Northern Europe) have been reported from the Czech Republic, where it was found closely to the town of Mnichovo Hradiště at an elevation of 230 m (Kubát, 1990). Altitudinal distribution is (880)–1300–2400 m in Spain, (800)–1600–2300 m in Italy, 1500–2450 m in Macedonia, 1400–2200 m in Bulgaria, and 1600–2250 m in Greece (Jäger in lit.), (750)–950–1610 m in Slovakia (Peter Turis in lit.; Jarolímek and Kliment, 2004).

Habitats

R. alpinus generally occurs in nutrient-rich natural, anthropogenic, and in their transitional types of habitats that are well supplied with water (Rechinger, 1957; Husáková, 1978; Dihoru and Dihoru, 1985; Ellenberg, 1996). Its natural habitats include river banks, flushes and rest places of charmoises or other big

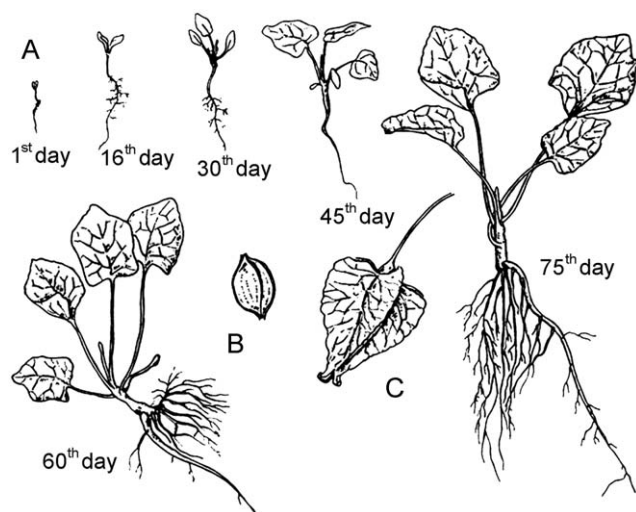


Fig. 2. Seed, fruit and seedlings of *Rumex alpinus*. A – gradual development of a seedling of *Rumex alpinus* 1, 16, 30, 45, 60 and 75 days after germination; B – achene; C – fruit consisting of three valves attached to the achene, and a pedicel. (Šmarda, 1963, with permission).

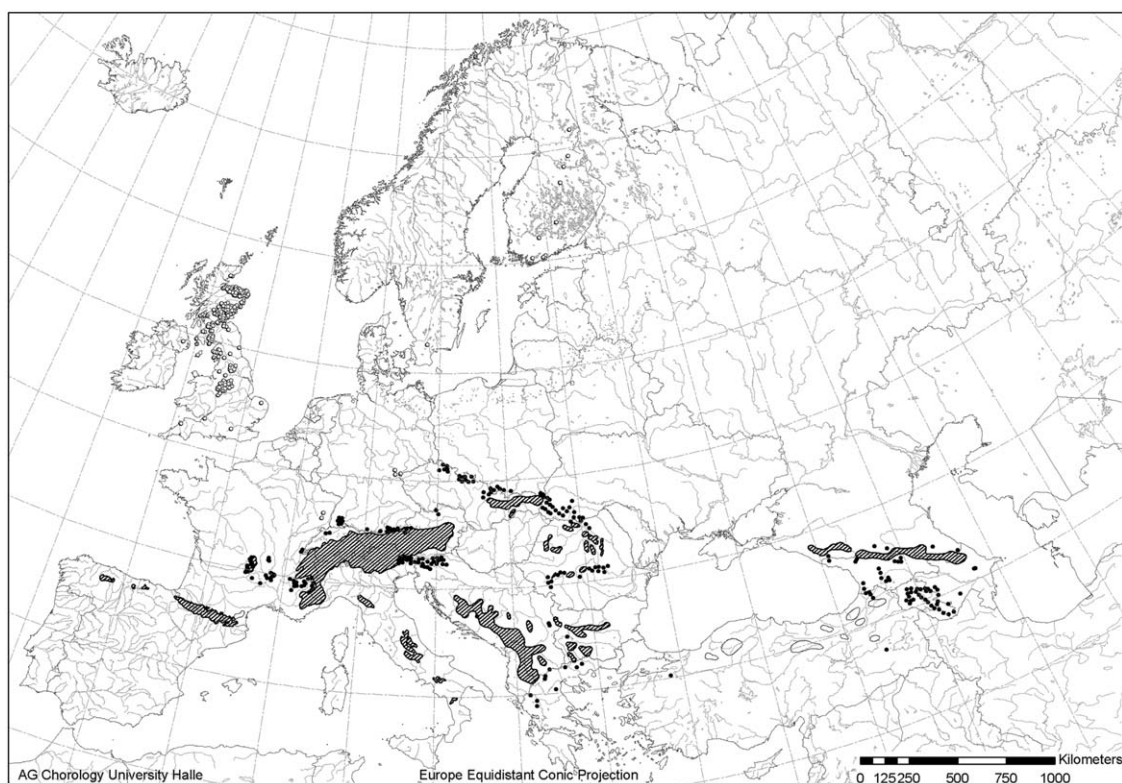


Fig. 3. General distribution of *Rumex alpinus*. Hatched areas and dots: natural occurrences (but introduced in Czechia, see text); open areas (not hatched) in Northern Turkey: occurrences without exact localisation; small circles: introduced occurrences. The species is also introduced in NE USA (Maine, Vermont) and in Java. Map drawn by E. J. Jäger, digitized by E. Welk (Halle).

ungulates (Ellenberg, 1996). It reaches the highest abundance at anthropogenic sites, such as abandoned mountain meadows, surroundings of sheep shelters, road ditches, dumps in the vicinity of mountain chalets, resting places of domestic animals and other sites where input of nitrogen is high or was high in the past decades (Dihoru and Dihoru, 1985; Gebauer et al., 1988; Klimeš, 1992; Ellenberg, 1996; Jarolímek and Kliment, 2004).

Stands of *R. alpinus* develop on soils ranging from acid to alkaline (but not highly acid, alkaline or salty), usually humus- and nutrient-rich, mesic-moist-wet throughout the year (eutric cambisol, dystic cambisol, calcic cambisol) and fine sandy, dusty, more or less well ventilated. These soils develop both on silicate and carbonate bedrock. Soils are prevailingly rich in nitrogen (Landolt, 1977; Ellenberg et al., 1992; Kliment and Jarolímek, 1995; Wilmanns, 1998). The supply of mineralized nitrogen ($\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$) may reach yearly 250 kg ha^{-1} , which exceeds the values obtained in other plant communities by a factor of 2–10 (Rehder, 1971). The soils have a medium to good supply of phosphorus (Wilmanns, 1998), high to extremely high supply of potassium, and a high supply of magnesium (Kliment and Jarolímek, 1995; Kutschera and Lichtenegger, 1992; Bohner, 2005). Javorka (2004) reports from Lenivá, Nízke Tatry, Slovakia in mg kg^{-1} : P (53.48), K (331.25), and Mg (261.86). The turnover of nitrogen and phosphorus is very efficient in *R. alpinus* stands (Rehder, 1982; Kobiv, 1986; Gebauer et al., 1988; Klimeš, 1992; Wilmanns, 1998). *R. alpinus* is usually missing on nutrient-poor soils (Landolt, 1977; Wagenitz, 1981).

Communities

R. alpinus is a strong competitor forming species-poor stands. Its broad leaves create a dense canopy above which tall flowering

shoots emerge (Šmarda, 1963; Kliment and Jarolímek, 1995; Bohner, 2005). The cover of *R. alpinus* is often close to 100% (Kliment and Jarolímek, 1995) but sometimes reaches up to 110% (Rudyshin and Tsarik, 1982). *R. alpinus* contributes to the total aboveground biomass of the community by about 90% (Malinovskij et al., 1982; Kobiv, 1984; Klimeš, 1992).

Numerous authors have reported about the species composition of communities dominated by *R. alpinus*, especially from Central Europe, the Alps and the Pyrenees, starting with Beger (1922). The number of units described at the association level is relatively low (Unar et al., 1985a, b; Jarolímek and Kliment, 2004), but for its vast world areal the great variability within associations is expected (Grabherr and Mucina, 1993). As the stands with *R. alpinus* are usually species-poor and lack species confined to them, some authors classified them as basal and derivative communities (Husáková, 1978; Grabherr and Mucina, 1993), i.e. communities placed out of the hierarchical structure of phytosociological units or associated with higher phytosociological units. Individual communities are differentiated either by subdominant species, or by the overall species composition, reflecting habitat conditions, stand age and extent of disturbance caused by domestic animals (Hadač, 1982; Oltean and Dihoru, 1986). Most species regularly occurring in stands of *R. alpinus* attain a low cover, except for several shade-tolerating herbs, such as *Stellaria nemorum* and *Urtica dioica*. Grasslands dominated by *Poa supina* (Grabherr and Mucina, 1993) or *Deschampsia cespitosa* are often invaded by *R. alpinus*, and both species may persist under the canopy of *R. alpinus*. *R. alpinus* causes reduction of species diversity in invaded communities (Hejda et al., 2009). *Urtica dioica*, *Rumex alpestris*, *Chaerophyllum hirsutum* and *Ch. villarsii*, *Geranium phaeum*, *Senecio subalpinus*, *Aconitum napellus* (Grabherr and Mucina, 1993; Ellenberg, 1996), *Peucedanum ostruthium* and *Veratrum album* (Wilmanns, 1998) are the most abundant species

among taller plants, whereas the ground layer is often formed by *Stellaria nemorum*, *Ranunculus repens*, *Silene dioica* and *Alchemilla* spp. (Hadač, 1982; Mirek and Skiba, 1984; Unar et al., 1985a, b; Oltean and Dihoru, 1986; Grabherr and Mucina, 1993; Kliment and Jarolímek, 1995; Kwiatkowski, 2003; Jarolímek and Kliment, 2004).

The best described and most widespread is the association *Rumicetum alpini* Beger 1922, reported from the Alps (Hess et al., 1976; Pott, 1992; Grabherr and Mucina, 1993; Wilmanns, 1998; Schubert et al., 2001; Fisher et al., 2008). Association *Rumici-Chenopodietum boni-henrici* (Br.–Bl.) Carrilo and Vigo 1984, reports Villar et al. (1999) from the Pyrenees.

Another approach of phytosociological classification of *R. alpinus* stands has been presented by Kliment and Jarolímek (1995), based on relevés from Slovakia. They distinguished two associations, the species-poor *R. alpini* Beger 1922 emend. Braun-Blanquet 1972, occurring in secondary habitats, and *Aconito firmi*–*R. alpini* Unar in Unar et al. (1985a, b), confined to semi-natural riparian habitats of mountain streams. Two altitudinally vicariating subassociations were described within ass. *A. firmi*–*R. alpini*: subass. *geranietosum sylvatici* occurs at higher elevations (1300–1450 m), whereas subass. *myosotidetosum nemorosae* is confined to lower elevations (950–1350 m).

Except for *Rumicetum alpini*, *R. alpinus* usually occurs in other subalpine and alpine communities e.g. in alliances *Arction*, *Adenostylion* or *Polygono-Trisetion* (Fenaroli, 1971; Oberdorfer, 1983; Wilmanns, 1998).

Response to abiotic factors

R. alpinus avoids shaded habitats, occurring chiefly in full light, and surviving in slight shade (Rechinger, 1957; Šmarda, 1963; Ellenberg et al., 1992) but may also persist in newly established forests for several years, if is sufficiently supplied with water (Landolt, 1977; Červenková, 2007). At low elevations it may suffer from high summer temperatures, even if regularly watered (Štastná, pers. obs.). After nutrient input from farming ceases, *R. alpinus* stands usually persist for several decades before they decline (Kopecký, 1973; Ellenberg, 1988; Klimeš, 1992; Nagy et al., 2003). Present populations of *R. alpinus* recorded from the Krkonoše Mts. originated more than 50 years ago when *R. alpinus* colonized the vicinity of farm houses and mountain chalets, after grazing intensity decreased or the number of domestic animals was reduced (Šourek, 1969). In Swiss national park, cattle grazing and fertilization was excluded in 1913 but the stands of *R. alpinus* still occupy previous areas (Ellenberg, 1996). *R. alpinus* can survive after 70 years from last fertilization (Grabherr and Mucina, 1993). On the other hand, the decline of *R. alpinus* was reported from farms, which were converted to non-agricultural residences in the Peak District, Great Britain (Preston et al., 2002).

Klimeš et al. (1993) assessed the capacity of *R. alpinus* to regenerate from rhizome fragments buried to depths of 5–30 cm. Leaves of rhizomes buried 30 cm under the ground failed to reach the soil surface and survived for a whole year on account of carbohydrate reserves. Leaves from rhizomes buried at a depth of 20 cm reached the soil surface after 4 months but the vitality of the emerging shoots was considerably lower than that of control plants. Rhizomes buried 20–30 cm deep produced fragile segments with internodes elongated up to 4 cm. The apical dominance was often broken and growth of several lateral buds was initiated. The content of total non-structural carbohydrates in rhizomes buried at a depth of 20 cm was close to zero in segments of the current year and about 25% in segments formed in the previous year. This contrasted with rhizomes buried 5 and 10 cm deep, where no differences between the two last segments were

found and the concentration of total non-structural carbohydrates was about 60%.

Except for above-mentioned factors, dynamic of *R. alpinus* stands is strongly affected by elevation. Plants at lower elevation are usually bigger, their stands reach a lower shoot density and a lower proportion of shoots is fertile (Štastná, pers. obs.), individual shoots of *R. alpinus* produce a lower number of leaves at higher elevations. The relationship between number of days with snow cover and mean number of leaves produced per year is almost linear, implying that new leaves appear at a constant rate of one leaf per 16 days. Even if the length of the leaves changes during a season from about 10 cm after snow melting to about 60–100 cm in June and then declines to about 20–30 cm in late autumn, the rate of emergence of new leaves remains remarkably constant (Klimeš, pers. obs.). Consequently, year-to-year variation in the annual number of leaves produced is usually well synchronised between stands differing in elevation (Štastná, 2005).

Life cycle and biology

Life cycle

The life form is a hemicryptophytic. Within the first season, *R. alpinus* seedlings develop a leaf rosette, shortened stem, and primary root system. Flowering shoots usually emerge in the third (in good conditions in the second) season of plant life. At that time the rhizome starts to branch producing a clone with phalanx growth form and with a dense leaf cover. Clone spread about 3–4 cm per year in mountain meadow in Krkonoše Mts. and disintegrate into physically independent fragments after about 13 years (Klimeš, 1992).

Spatial distribution

Stands of *R. alpinus* range in size from about one to several hundreds of square metres (Klimeš, 1992; Kliment and Jarolímek, 1995; Bucharová, 2003). Shoots of *R. alpinus* are in a monotypic stand are distributed randomly (Klimeš, 1992). Using spatially implicit modelling, it has been shown that in a homogeneous environment where mortality and branching frequency is random, this spatial distribution develops in about 5 years, independently of the original distribution of the ramets (Klimeš, 1992). The stands of *R. alpinus* on stream banks are usually sparser and less layered than stands on meadows due to frequent floods and shallow soils (Červenková, 2007).

Biomass production

Seasonal changes in leaf area and biomass of *R. alpinus* were studied in the Ukrainian Carpathians at 1370 m above sea level (Kobiv, 1984). At the end of June the maximum value of the leaf area index rose to 6. In August it declined to one half, due to severe herbivory by *Gastrophysa viridula* (Chrysomelidae, Coleoptera). Almost the same leaf area index values have been reported by Tsarik (1981): 5.5 ± 0.4 . We obtained a considerably lower value of 3.3 at the end of June 1989, in the Krkonoše Mts., Czech Republic, at 1150 m (Fig. 4). A similar value, 3.25, was estimated by Rudyshin and Tsarik (1982) in June in the Ukrainian Carpathians. Vertical leaf area distribution in *R. alpinus* is unimodal until side branches start to produce their leaves, which form a lower layer in *R. alpinus* stands, and the vertical distribution becomes bimodal (Fig. 4). At the end of vegetation season, leaves of side shoots either reach canopy of the stand or branches become dormant and vertical leaf area distribution becomes unimodal again.

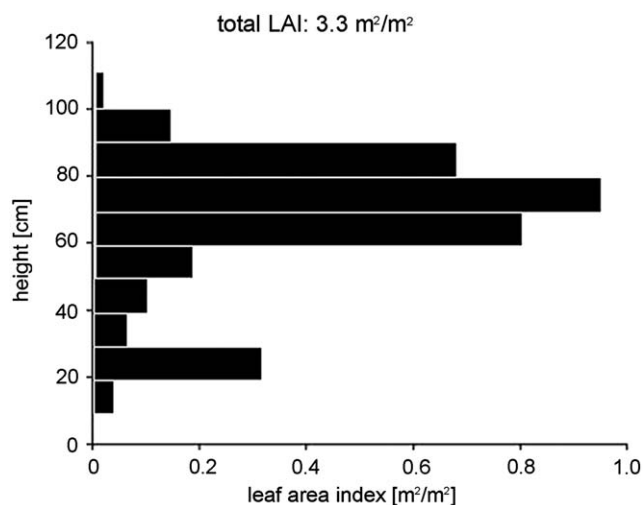


Fig. 4. Vertical distribution of leaf area index in *Rumex alpinus* (a plot 1 m² in size was harvested and analysed in continuous stand dominated by *R. alpinus*, August 1989, Krkonoše Mts., 1150 m above sea level).

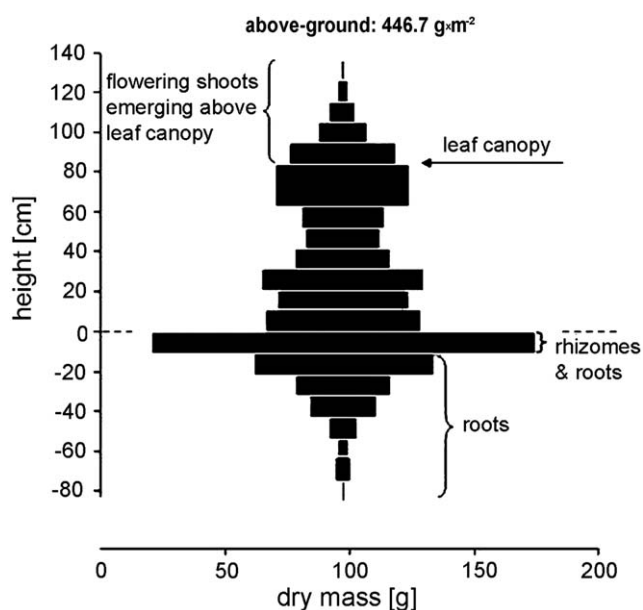


Fig. 5. Vertical distribution of dry mass in *Rumex alpinus* (a plot 1 m² in size was harvested and analysed in continuous stand dominated by *R. alpinus*, August 1989, Krkonoše Mts., 1150 m above sea level).

Total dry mass of *R. alpinus* stands estimated in the Ukrainian Carpathians was 2.02–2.05 kg m⁻², of which 57.5% belonged to above-ground biomass (Tsarik, 1981). On the other hand, 2.2 ± 0.12 kg of below-ground dry mass has been reported by Antosiak (1987). A maximum above-ground biomass of 600 g m⁻² estimated at the end of June was reported from the same area by Kobiv (1984). This value declined to about a half in September. In the Krkonoše Mts., Czech Republic, we obtained on 26 August 1989 at 1150 m a.s.l. slightly lower value of 447 g m⁻² (Fig. 5). Below-ground biomass in the same stand was 1080 g m⁻², corresponding to about 70% of total biomass. The major part of it was formed by rhizomes (776 g m⁻²; 72%), which were situated in the uppermost layer of the soil (0 to -10 cm). Roots (306 g m⁻²; 28%) reached a depth of about 80 cm but the major part of their biomass was located in a depth of up to 40 cm (Fig. 5). Ellenberg (1996) reports the annual production of dry above-ground biomass more than 5 t ha⁻¹.

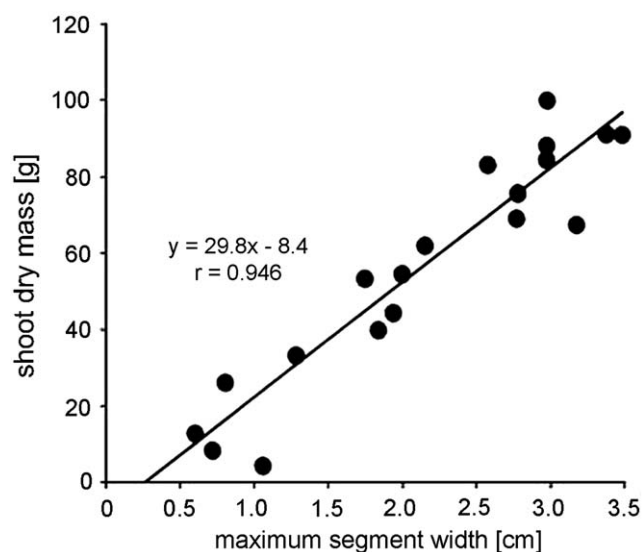


Fig. 6. The relationship between maximum width of an annual increment of a rhizome of *Rumex alpinus* and dry mass of its shoot in August 1989 (shoots were harvested and analysed in continuous stand dominated by *R. alpinus*, Krkonoše Mts., 1150 m above sea level).

The dry mass of *R. alpinus* shoots is strongly and linearly correlated with the maximum width of annual increments (Fig. 6). Therefore, under the reasonable assumption of a negligible decomposition of new rhizome segments, the maximum biomass of a stand within one season can be estimated several years back, using ad hoc measurements of rhizome segments.

Phenology

Leaves of *R. alpinus* start their growth shortly after snow melting (Kutschera and Lichtenegger, 1992; Bohner, 2005). Depending on elevation and timing of snow melting, the onset of vegetative growth may be shifted several weeks (Štátná, unpublished).

The plants develop their leaves during the entire vegetation season. Blades of the first leaves are small and their petioles are short, about 5 cm. The biggest leaves develop in the middle of the season, at the onset of flowering. After that, the size of new leaves is slowly reduced, until the end of the season, when they are damaged by the first strong frosts (Šmarda, 1963; Kliment and Jarolímek, 1995). Depending on the length of the season, individual apical meristems produce about 6–25 leaves, the number of leaves per year is affected by mesoclimatic factors and year-to-year variation is synchronized in different stands in one mountainous range (Fig. 7). In closed-canopy stands dominated by *R. alpinus* about 3(–5) leaves per shoot are alive (Šmarda, 1963) at any time of the year. Thus, the oldest leaves die off at the same speed as new leaves develop in the course of the season.

R. alpinus flowers usually from June to August; mostly only once per season and the flowering of particular populations is broadly synchronized. Fruiting extends from July to August. Ripe seeds drop down, usually together with the valves, in late summer or in autumn; some fruits may persist on stalks until next spring (Müller-Schneider, 1986; Kliment and Jarolímek, 1995).

Reproduction

R. alpinus reproduces by vegetative multiplication and generatively. Vegetative multiplication plays a prominent role in closed-canopy stands and along their margins. The generative way

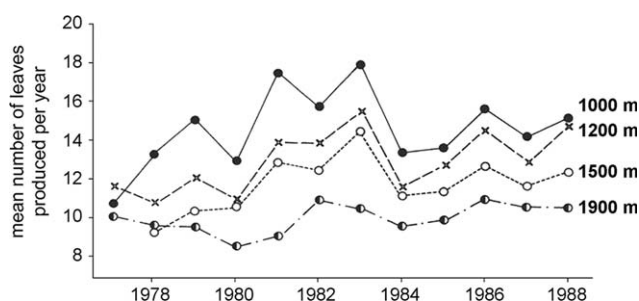


Fig. 7. Growth synchronisation between four populations of *Rumex alpinus* along an altitudinal gradient in the Low Tatra Mts. from 1977 to 1988. Mean number of leaves per year increment was counted for at least 10 rhizomes in each altitude.

is important mostly for colonizing new habitats and disturbed patches within already established stands (Kutschera and Lichtenegger, 1992; Bucharová, 2003; Červenková, 2007).

Individual shoots do not produce generative organs every year (Low Tatra Mts., pers. obs.). Generative reproduction is enhanced by excessive nutrients and favourable climatic conditions in the current and previous year. Strong intraspecific competition in closed-canopy stands may significantly reduce the frequency of flowering and fruiting in comparison with newly established patches in meadows (Klimeš, 1992).

Flowering of *R. alpinus* takes usually several weeks. *R. alpinus* is a reputedly anemophilous plant, similarly to other *Rumex* species (Jäger and Werner, 2005). The large amounts of pollen produced by flowering plants, however, attracts numerous pollen-feeding and pollen-collecting insects, such as syrphid flies and bumblebees (Klimeš, 1994). These may transfer pollen among individual plants on hairs of their legs and bodies (Kendall and Solomon, 1973; Holloway, 1976), thereby taking part in the gene flow of *R. alpinus* populations (Klimeš, 1994), but anthophyllous insects are not adapted to collect the smooth pollen from overhanging stamens of *R. alpinus* (see also section “Herbivores and pathogens”).

The production of fruits is very high; reported values for one inflorescence are as follows: 1500–2000 (Antosiak, 1987; Rudyshin and Tsarik, 1982) to 4000 (Javorka, 2004), to 5000 (Malinovskij et al., 1982; Zhiliaev, 2003). About 80% of flowers usually develop fruits (Antosiak, 1987).

Density of flowering and fruiting shoots ranges from 3 to 5 m⁻² (Bucharová, 2003) to 8 m⁻² (Malinovskij et al., 1982). Total shoot density ranges from 22 m⁻² (Tsarik, 1981) to 35 m⁻² (Antosiak, 1987). Due to this variation, the estimates of seed production vary considerably. While Klimeš (1992) gives an estimate of 11 500 seeds m⁻², Rudyshin and Tsarik (1982) reported 16 000 and Malinovskij et al. (1982) estimated a number of 30–40 000 seeds m⁻².

The seeds mature from the inflorescence base to the top. Soon after seed ripening, stalk branches may break off (Šmarda, 1963) and only a few of them remain protruding above the leaf canopy, losing seeds gradually, until winter or even next spring. This enables spreading of seeds within the tightly attached valves on snow surface. An important way of diaspore spreading is by streams. A detailed assessment of *R. alpinus* distribution along water flows in the Krkonoše Mts. (Czech Republic) indicates a decisive role of hydrochory in the dispersal of the species (Bucharová, 2003). Water from melting snow may also transport seeds, as indicated by the distribution of *R. alpinus* in the Ukrainian Carpathians (Komendar and Lishchuk, 1991; Bucharová, 2003). Transport of seeds in sheep fur has been reported by Komendar and Lishchuk (1991), dyszoochory by birds: *Tetrao urogallus*, *T. terix*, *Carduelis spinus* and *Passer domesticus*, endozoochory is presumable through cattle and goats (Müller-

Schneider, 1986; Kutschera and Lichtenegger, 1992). The role of wind in spreading individual achenes is limited, due to the relatively large size of the achenes; however, achenes are effectively spread by wind together with the valves, functioning as wings, but Müller-Schneider (1986) presents the necessary velocity of wind 1.4 m s⁻¹ for vacating the seeds and determines them as pterometeorochores. Kubátová (1994) found that *R. longifolius*, a species with similar achenes and valves, spreads in the direction of prevalent winds.

R. alpinus may spread also by rhizome fragments, e.g. along streams or avalanche paths. The effect of rhizome fragmentation was studied experimentally by Komendar and Lishchuk (1991). They cut rhizomes of *R. alpinus* into fragments differing in size, planted them in autumn in the field and evaluated their regeneration next spring. Most fragments successfully regenerated and flowered. If the rhizome fragments were planted in spring, success was much lower. Only 3% of 3 cm long fragments survived, 19% of 3–5 cm long fragments, 59% of 5–7 cm long fragments and 74% of 7–10 cm long fragments survived the experimental treatment. About 25% of regenerated plants flowered in the first year after the fragmentation, independently of rhizome size.

Seed bank

Seed density, estimated in the soils of meadows in the Krkonoše Mts. as the number of germinating seeds, ranged from 3200 m⁻² (Bucharová, 2003) to 6000–18 000 m⁻² (Handlová and Münzbergová, 2006). Another estimate of 11 500 seeds m⁻² was obtained in the Ukrainian Carpathians (Malinovskij et al., 1982). The high variation corresponds to differences in density of fertile shoots. According to Seed bank of *R. alpinus* may be classified as long-term persistent (sensu Thompson et al., 1997).

Germination

Seeds of *R. alpinus* do not possess a primary dormancy and their germination rate is often > 90% (Štastná, unpublished data). Seedlings of *R. alpinus* hardly establish in well-managed dense grasslands, presumably due to their low tolerance to shading and interspecific competition (Cavers and Harper, 1964; Klimeš, 1992; Červenková, 2007). It has been estimated that only 3–5% of light penetrates through the leaf canopy of *R. alpinus*. Due to that, the probability of establishment of *R. alpinus* seedlings in stands dominated by it is as low as 10⁻⁹ (Klimeš, 1992).

Germination of seeds is significantly supported by pasture of livestock, mostly by cattle whose hoofs disturb the cover and excrements create an ideal microhabitat for germination.

We studied the effect of light intensity and temperature on germination of *R. alpinus* in experimental conditions. Ripe seeds of *R. alpinus* collected in August in the Krkonoše Mts. were stored at room temperature for 6 months before the experiment started. After that, 50 seeds were placed on a wet piece of filter paper in each Petri dish, 9 cm in diameter with three replicates. The Petri dishes were placed on crossed gradients of light intensity (four levels: 200, 500, 800 and 1000 μmol m⁻² s⁻¹) and temperature (15 levels: 8–29 °C; for details concerning the crossed gradients, see Kviderová and Lukavský, 2001). Germinating seeds were removed daily until day 50. The first seeds started to germinate on day 4. Germination at a temperature lower than about 10 °C was delayed by up to 5 days. The germination was finished after 15–25 days, firstly at higher temperatures and full light intensity. Mean germination rate was relatively low, about 40%, possibly due to the relatively long storage of the seeds before the experiment started (Table 1) as just-after-ripening seeds have more than 95%

Table 1Mean percentage of *R. alpinus* seeds germinating after 50 days along cross-gradients of temperature and light intensity ($n=3$).

		Temperature (°C)										
		8	10	12	14	16	18	20	22	24	26	28
Light intensity ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	1000	–	–	–	21	26	–	24	39	35	21	19
	800	–	–	19	36	42	38	41	62	41	–	–
	500	–	16	28	38	43	29	33	43	–	–	–
	200	5	8	12	32	38	29	31	–	–	–	–

germination. Stored seeds of *R. alpinus* lose their germination capacity slowly, because 13-year-old seeds still germinate regularly (Rechinger, 1957; Wagenitz, 1981; Bucharová, 2003). Bucharová (2003) reported a 17% decrease in germination in seeds stored for 1 year.

Germination rate of *R. alpinus* is not affected if far-red radiation is filtered out (Bucharová, 2003), indicating that under a dense leaf canopy, light intensity rather than light quality is the limiting factor (Bucharová, 2003). Only small percentage of seeds (3–5%) germinates in full dark at room temperature (Klimeš, unpubl.).

Response to competition and management, other experiments

Interspecific competition

R. alpinus is usually a strong dominant in its stands (e.g. Šmarda, 1963; Malinovskij et al., 1982; Klimeš, 1992). Its successful spreading is enhanced by effective suppression of other species by shading and by fast occupation of both above- and below-ground space (Šmarda, 1963; Bohner, 2005). Therefore, only shade-tolerant species and gap specialists may persist in *R. alpinus* stands (Bohner, 2005); details are in section “Communities”. Only during the short spring period (usually taking maximally 2 months), before closing of the *R. alpinus* canopy, light availability is reasonably high. However, the efficient utilisation of large carbohydrates reserves allows early and rapid regrowth in spring, enabling to keep the prominent position of *R. alpinus* in its stand (Klimeš et al., 1993; Bohner, 2005). The long persistence of the mighty rhizomes is also important in the competitive strength of *R. alpinus* (Husáková, 1978).

Control by management

Suppression of *R. alpinus* stands is often desirable, especially in protected areas where its extensive spread may reduce species diversity and rare plants can be endangered due to its expansion. In an experiment carried out in the Ukrainian Carpathians, three intensities of mowing, trampling and rhizome cutting were used and survival of plants, biomass and cover of plant canopy were assessed. The largest reduction of *R. alpinus* was achieved in plots mown every 10 days. The mowing resulted in a reduction of *Rumex* cover. Consequently, seedling establishment from the seed bank was promoted. Mowing twice in a year increased seedling abundance by about 30% in comparison with the control. Seedling survival until next year was 20% in contrary to intact stand of *R. alpinus* where no survival was observed. Similarly, the treatment in which rhizomes were fragmented induced vegetative regeneration of *Rumex* plants (Tsarik, 1987). Unfortunately, vegetation response was monitored for one season only.

R. alpinus shows an exceptional vitality and regeneration ability after leaf removal. Already 1 day after a stand of *R. alpinus* plants was cut, leaves started to develop (Šmarda, 1963). During next days the plants increased their height by 2 cm per day and within 10 days the closed canopy was re-established. Fast regeneration of mown stands was noted by Antosiak (1987),

who reports that *R. alpinus* reached a height of 40 cm in 20 days after mowing of a stand. Also repeated defoliation is tolerated by *R. alpinus* rather well (Bohner, 2005).

Successful suppressing is only possible through regular mowing and removing of cut biomass. *R. alpinus* does not form large patches and never becomes a dominant in managed grasslands (Ellenberg, 1996; Bucharová, 2003).

Bucharová (2003) and Jiříšřtě and Mládková (1998) reported on results of chemical control of *R. alpinus* stands in Krkonoše Mts. treated by the 3–5% solution of herbicide Roundup Biaktiv, used 3 times in a season (July–September). After the treated *R. alpinus* stands were damaged, establishment of a grassland was promoted by sowing seeds of several grasses (*Alopecurus pratensis*, *Agrostis capillaris* and *Festuca rubra*), which established successfully. Even if numerous seeds of *R. alpinus* germinated from the seed bank in the treated plots, young plants were soon suppressed by the grasses. Three years later, only a few small plants of *R. alpinus* persisted in the stands whereas the grasses became dominant. Use of mulching with hay containing mature seeds of meadow plants instead of sowing grass seeds, or covering the plots with a geo-textile was successful management as well (Jiříšřtě, 2000). Application of regular mowing, which promote tillering of grasses so that dense swards develops, in which *Rumex* seedlings cannot establish any more is necessary (Kutschera and Lichtenegger, 1992; Bucharová, 2003).

Potential biocontrol agents

Gastrophysa viridula (Chrysomelidae, Coleoptera) is a natural enemy of docks in Europe (Mohr, 1966; Martínková and Honěk, 2004) and its subspecies *caucasica* Jolivet, occurs in Turkey. The beetle is considered as important potential biocontrol agent (Aslan and Özbek, 1995, 1999; Hatcher et al., 1997). Although the leaf herbivory by *G. viridula* decreases the vigour of *Rumex* plants, it is not capable of eradicating the plants, especially at higher elevations (Tsarik, 1986). The potential disadvantage of *G. viridula* as a biocontrol agent is its short flight distance, which is usually less than 10 m (Martínková and Honěk, 2004).

The effect of herbivory can possibly be enhanced by other biocontrol agents. The rust *Uromyces rumicis* (Pucciniaceae) colonising *Rumex obtusifolius* and *R. crispus* leaves is a candidate, but no data about its effects on *R. alpinus* are available.

Herbivores and pathogens

Trophic relationships in a *R. alpinus* stand were studied by Rudyshin and Tsarik (1982) in the Ukrainian Carpathians. They found larvae and adults of *G. viridula*, *Otiorhynchus niger* and *Otiorhynchus* sp. as the most important herbivores feeding on leaves of *R. alpinus*. On the average, they found 5–7 adult beetles of *Gastrophysa* and 1–2 adult beetles of *Otiorhynchus* per plant. The beetles were most active in June and July, when they reduced the leaf area to about 20% (*Gastrophysa*) and 75% (*Otiorhynchus*), respectively. Two species of mammals have been found to feed on

above-ground plant parts of *R. alpinus*. Leaves were eaten by *Microtus subterraneus* and flowering stems by *Microtus agrestis*.

Among herbivores feeding on pollen of *R. alpinus*, several species of Syrphidae have been reported: *Myagtropus florea* (Rudyshin and Tsarik, 1982), *Syrphus torvus*, *Parasyrphus lineola* (Klimeš, 1994), and the bumblebee *Bombus terrestris* (Klimeš, 1994). The mean percentage of *Rumex*-type pollen in crops and intestines of syrphid flies was nearly 90% in *Syrphus torvus* and 67% in *Parasyrphus lineola*, indicating that these syrphids may prefer this type of food when it is available in excessive amount. Similarly, *Bombus terrestris*, a bumblebee species regularly collecting pollen from plants with corolla tubes, was repeatedly recorded to collect pollen from *R. alpinus* as well. The percentage of *Rumex* pollen in its pollen baskets ranged from 93% to 96% (Klimeš, 1994).

Seeds of *R. alpinus* are consumed by several species of mammal (*Apodemus sylvaticus*, *A. flavicollis*, *Muscardinus avallanarius*, *Dyromys nitedula* and *Sicista betulina*) and by omnivorous birds (*Acanthis cannabina*, *Fringilla coelebs*, *Emberiza citrinella* and *Prunella modularis*; Rudyshin and Tsarik, 1982). Rhizomes and roots are consumed by larvae of beetles (*Otiorhynchus niger* and *Otiorhynchus* sp.) and by mammals (*Rattus norvegicus* and *Arvicola terrestris*). Other mammals, *Microtus subterraneus* and *M. agrestis*, specialise on below-ground organs of *R. alpinus* during winter (Rudyshin and Tsarik, 1982).

The following animals have been reported as herbivores feeding on *R. alpinus*:

Coleoptera: Chrysomelidae: *Oreina elongata* Suffrian (larvae). Survival on *R. alpinus*, as a potential host plant, is limited (Ballabeni and Rahier, 2000).

Coleoptera: Curculionidae:

- *Otiorhynchus corvus* Boheman. Larvae of this polyphagous species feed on young roots of *R. alpinus* in the Beskydy Mts. and in the W Carpathians (Knutelski, 2005) (leg. P. Štátná, det. R. Borovec).
- *Plinthus tischeri* Germar. Distributed in the Carpathians and in the Sudetes (Smreczyński, 1968), Freistaat Thüringen, Germany (Knutelski, 2005) (leg. P. Štátná, det. R. Borovec).
- *Plinthus findeli* Boheman. So far collected on *R. alpinus* only, distributed in the Czech Republic, Pyrenees, the Alps and W Balkans (Smreczyński, 1968).
- *Plinthus sturmii* Germar. – Distributed in Austrian Alps, Bosnia, Albania, Carpathians, and Sudetes (Knutelski, 2005)
- *Donus comatus* Boheman. – Distributed in Carpathians, Sudetes, Alps, and Balkans (Knutelski, 2005)
- *Rhinoncus pericarpus* L. This oligophagous species has been collected on several *Rumex* species, including *R. alpinus*, and is distributed in the Palearctics and in North America, up to an elevation of 1500 m (Smreczyński, 1974).

Lepidoptera: Hepialidae: Caterpillars of *Hepialus humuli* L. were found in rhizomes of *R. alpinus* (leg. P. Štátná, det. K. Spitzer). The genus *Hepialus* generally comprises polyphagous species, so that other mountain species, such as *H. fuscomelubosus* DeGeer and *H. carna* Denis and Schiffermüller, may feed on *R. alpinus* as well (de Freina and Witt, 1990; Joss, 1992; Günter, 1993).

Homoptera: Aphids were observed on young leaves of *R. alpinus* (pers. obs.).

Allelopathy

Komendar and Lishchuk (1991) recorded reduction of germination rate of *Dactylis glomerata*, *Lolium perenne*, *Trifolium pratense*, *T. repens* and *Capsella bursa-pastoris* of 18–67% in

comparison with the control, when water solutions from rhizomes/roots, leaves and flowers/seeds from *R. alpinus* were added to the substrate.

Mycorrhiza and fungi

Roots of *R. alpinus* are colonised by vesicular-arbuscular mycorrhizal (VAM) fungi facultatively (Harley and Harley, 1987a, b).

The following fungi have been recorded on *R. alpinus*:

Ustilaginales – *Ustilago parlatorei* A. A. Fisch. Waldh.: Scholz and Scholz (1988), Vánky (1994), Klenke (1998), Zwetko and Blanz (2004).

Uredinales – *Uromyces rickerianus* Arthur: Farr et al. (1989)

- *Uromyces rumicis* (Schumach.) G. Winter (Europe, Gäumann, 1959),
- *Schroeteria alpinus* Magnus (Europe, Gäumann, 1959),
- *Puccinia phragmitis* (Schumach.) Lönn. (Aecidia; Europe, Gäumann, 1959),
- *Ramularia rubella* (Bonord.) Nannf. (Syn.: *R. circumfusa* Ellis & Everh.) (Europe, widespread, Braun, 1998),
- *Ramulla rumicis* Kalchbr. & Cooke (Armenia; Braun, 1998),
- *Phacopsora alpina* (J.Schröt.) Arthur: Arthur (1917).

Ascomycetes:

- *Leptosphaeria macrospora* (Fuckel) Thüm., anam. *Scolecosporella bernardiana* (Sacc.) Sivan.: Sivanesan (1984).
- *Phaeosphaeria nigrans* (Roberge in Desm.) L. Holm: Leuchtmann (1984).
- *Venturia rumicis* (Desm.) G. Winter: on living and fading leaves in Europe and North America (Müller and von Arx, 1962), in Greece (Pantidou, 1973).

Physiological data

R. alpinus requires an acclimation to prevent inhibition of CO₂ fixation by UV-B radiation. Reduced photosynthetic CO₂ fixation of non-acclimated *R. alpinus* plants seems to be due to the effect of UV-B radiation on stomatal conductance. Chlorophyll content was not affected by the applied UV-B levels (Hübner and Ziegler, 1998). In contrast to many other plants, detrimental effects of UV-B on *R. alpinus* are not masked if the plants are subjected to nutrient stress (Bogenrieder and Doute, 1982).

R. alpinus is plant species with a high absorption capacity for nitrate and potassium. Because of selective uptake from the soil solution, *R. alpinus* stores N, P, S, K, and Cl in basal leaves in considerable amounts, and discriminates against other elements, especially calcium (Bohner, 2005).

Biochemical data

Coloration of young and autumnal leaves of *R. alpinus* is caused by cyanidin monoside (Price and Sturgess, 1938). A detailed survey of secondary compounds of *R. alpinus* from the Ukrainian Carpathians was published by Gritsik et al. (1997). They analysed phenolic compounds, anthraquinones, flavonoids, polyphenols, anthocyanins, organic acids, ascorbic acid and vitamin K in above-ground and below-ground biomass in the course of a vegetation season. They concluded that the content of secondary compounds in *R. alpinus* is lower than in *R. confertus*, so that the first species can be recommended only as a supplementary source of these compounds. In contrast, the concentration of oxyanthraquinones

estimated in *R. alpinus* plants from Georgia reached 3.58%, and were higher than in three other studied *Rumex* species (*R. obtusifolius*, *R. crispus* and *R. acetosa*; Chumburidze, 1950).

Free and bound anthraquinones, and tannins were analysed in the below-ground biomass of several *Rumex* species by Czetsch-Lindenwald (1943a, b). He found that there are considerable fluctuations in content in the course of a season. In comparison with other *Rumex* species, the concentrations of anthraquinones and tannins were close to the mean values calculated for all analysed species.

Laxative anthraquinone derivatives were analysed in rhizomes and roots of *R. alpinus* also by other authors (Babulka, 1980; Babulka et al., 1982; Milkowska et al., 1997). Babulka (1980) compared 7 types of anthraquinone derivatives extracted from *R. alpinus* rhizomes and from roots of rhubarb. The results showed that the concentration of anthraquinone derivatives in *R. alpinus* rhizomes is about 3%, which does not differ from rhubarb, so that *R. alpinus* can be utilized as an alternative source of anthraquinone derivatives.

Concentration of tannins in roots and rhizomes of *R. alpinus* reaches nearly 12%, which is comparable to other *Rumex* species, in some areas utilized as a source of these compounds (Budzyk, 1957).

The production of acetate-derived hydroxyanthraquinones, -dianthrones, -naphthalenes and -benzenes in tissue cultures from roots of *R. alpinus* depended on the type of medium and presence of kinetin in tissue culture (van den Berg and Labadie, 1981); the process of biosynthesis of acetate-derived naphthol (2-acetyl-3-methylnaphthalene-1,8-diol) in *R. alpinus* was described in detail by Bauch et al. (1975).

The main storage compound accumulated in *R. alpinus* rhizomes is starch. Concentrations of total non-structural carbohydrates (TNC) in the dry mass of annual increments produced in the current year reaches 68% at the end of a growing season (Klimeš et al., 1993). In an experiment carried out ex situ, TNC concentrations reached about 50% (Klimešová and Klimeš, 1996). This measurement was done in March, before the next season started, in contrast to the previous experiment where TNC was estimated before winter. The difference in TNC can therefore be explained by winter respiration of the rhizomes. The lowest concentration of TNC in the latter experiment was found in annual increments of the previous year (42.5%), the highest in the annual increments of the year before that (54.4%). For older increments, the TNC concentrations slowly decreased, with 48.6% estimated in increments 6 years old (Klimešová and Klimeš, 1996).

Genetic data

The number of chromosomes counted on plants from various regions was invariably $2n=20$, with only one $2n=18$ count (Table 2), which is doubtful. As basic chromosome numbers for *Rumex* have been reported to be 7, 8, 9 and 10 (Kihara and Ono, 1926; Darlington and Wylie, 1955), *R. alpinus* is a tetraploid species, similarly to several other species belonging to the same subgenus (Ichikawa et al., 1971).

Hybrids

Two hybrids of *R. alpinus* have been reported:

R. alpinus × *obtusifolius*: *Rumex* × *mezei* Haussknecht (= *R. alpinus* × *obtusifolius* var. *microcarpus*: *R. austriacus* Teyber; = *R. rhaeticus* Brügg.): from Austria, Germany, Switzerland (Rechinger, 1957) and Czech Republic (Kubát, 1990)

R. alpinus × *longifolius* subsp. *sourekii* (= *Rumex* × *corconticus* Kubát) – so far a single record from Pec pod Sněžkou, Krkonoše Mts. (Kubát, 1990)

Table 2

Chromosome numbers of *Rumex alpinus*.

Chromosome number	Locality	Reference
$2n=20$	Botanical Garden, Oslo, Norway	Kihara and Ono (1926)
$2n=20$	Botanical Garden, Liège, Belgium	Jaretsky (1928)
$2n=20$?	Takenaka (1941)
$2n=18$	Austria	Tischler (1950)
$2n=20$	Central Pyrenees	Larsen (1954)
$2n=20$	Romania: near Sibiu	Löve (1967)
$2n=20$	Slovakia?	Májovský (1970)
$2n=20$	(Seeds obtained from Botanical Gardens)	Ichikawa et al. (1971)
$2n=20$	Slovakia: Západné Karpaty, Babia Hora	Májovský (1974)
$2n=20$	Poland	Mizianty et al. (1983)
$2n=20$	Ukraine	Pashuk (1987)
$2n=20$	Bulgaria	Stoyeva (1987)
$2n=20$?	Huber and Baltisberger (1989)
$2n=20$	Poland	Jankun (1989)
$2n=20$	Yugoslavia	Baltisberger (1990)
$2n=20$	Turkey	Baltisberger (1991)
$2n=20$	Czech Republic: Špindlerův Mlýn	Měsíček and Jarolímová-Javůrková (1992)
$2n=20$	Austria	Dobeš et al. (1997)

Utilisation

In alpine areas, *R. alpinus* was utilized by humans in historical times (Rechinger, 1957; Hegi et al., 1977). High values in pollen diagrams from the Italian Alps indicate an increase in abundance at about 2400 BP (Maude and Moe, 2005). It was used for various purposes; the species possibly belongs to the oldest known vegetables (Brockmann-Jerosch, 1921). The plants were cultivated in gardens of mountain dwellers and used as a surrogate of sauerkraut or spinach. The stems were peeled and used instead of rhubarb, or eaten fresh or put into cakes, biscuits, and puddings (Dickson and Dickson, 2000). Boiled plants were used as a fodder for pigs and goats (Brockmann-Jerosch, 1921). The leaves were used for packing butter in Tyrol and in some parts of the Carpathians (Kopecký, 1973). For medicinal purposes, *R. alpinus* was used in the Alps as a surrogate of less accessible Polygonaceae species (*Radix Rhaipontici montani* or *Radix Rhei Monachorum*) and was cultivated in monastery gardens for that purpose (Rechinger, 1957). As a laxative it is marginally used even in current medicine (Babulka, 1980). The plant was valued for its supposed curative effects already in the Middle Ages (Kopecký, 1973) and is used in local medicine to treat stomach problems in Bulgaria and Ukraine (Budzyk, 1959; Topalov et al., 1983). Plants of *R. alpinus* are used in Turkey to treat constipation, diarrhoea and eczema. In assays against 121 strains belonging to 52 bacterial species, Ozturk and Ozturk (2007) found antibacterial potency in methanol extracts of aerial parts of the plant, may for that reason were large leaves used for cooling of diseased or feverish parts of skin in Oberbayern (Hegi et al., 1977).

The herb is avoided by cattle (Bohner, 2005), probably due to the poisonous effect corresponding to that caused by other species of *Rumex* sect. *Lapathum* (Roth et al., 1994; Maude and Moe, 2005). However, it is eaten by goats (Ellenberg, 1988). *R. alpinus* plants are, according to Rechinger (1957), consumed by cattle only if other food is not available.

The deep orange colour of rhizomes of *R. alpinus* was used in the central Alps for colouring fabric (Wagenitz, 1981).

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