5.4. POPULATION ECOLOGY OF *RUMEX OBTUSIFOLIUS*

Leoš Klimeš

Introduction

Related species, species aggregates and the species consisting of two or more lower taxonomic taxa serve as ideal models for comparative studies as the differences among sister taxa which have been phylogenetically relatively recently isolated should reflect adaptations to their specific habitat (Kuiper & Bos 1992). Unfortunately, the great variation in the species, described by taxonomists, is sometimes not respected by population ecologists. This is the situation with *Rumex obtusifolius*, a common weed which has been intensively studied by numerous researchers since the 1960s. Four subspecies differing in their geographical distribution are usually considered. However, this variability has not been respected in population studies so that it is often not clear with which subspecies a particular paper deals.

The available data on ecological differentiation between *R. obtusifolius* subspecies based on their distribution in an entire area (Rechinger 1964) and on their local distribution (Klimeš 1989) suggest that there are marked differences between the subspecies in their distribution along basic environmental gradients. Thus, a differentiation in ecological demands of *R. obtusifolius* subspecies can also be expected. The aim of this study was to test the effect of the most important biotic and abiotic factors identified in the floodplain of the Lužnice River on growth and reproduction of *R. obtusifolius* with a special attention to differentiation between *R. obtusifolius* subspecies *obtusifolius* and *R. obtusifolius* subspecies *sylvestris* (hereafter referred to as *R. *obtusifolius* and *R. *sylvestris*). First, the variation of *R. obtusifolius* in the studied area is described and the identified types are mapped. Using multivariate methods, the major environmental factors governing the distribution of individual types are suggested. Then, the effects of these environmental and biotic factors on the subspecies of *R. obtusifolius* are described. Finally, an attempt is made to predict the distribution of *R. obtusifolius* in the study area for the next several decades.

The plant

R. obtusifolius L. is a perennial herb with a tap root, a rosette of leaves, one to several stems bearing numerous leaves, and a great number of small greenish flowers and fruits inserted into three enlarged perianths (valves). *R. obtusifolius* is an anemophilous, self-compatible species. Most of its flowers are hermaphroditic and protandrous (Cavers & Harper 1964; Foster 1989). *R. obtusifolius* is a common weed of European origin which has secondary spread over all continents except Antarctica. Four infra-specific taxa with partly overlapping distribution are usually recognised (Rechinger 1932; Rechinger & Akeroyd 1992). Their taxonomic value is, however, uncertain as individual specialists consider them as being either (i) independent species

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(Czerepanov 1981), (ii) subspecies (Rechinger & Akeroyd 1992 and many others) or (iii) varieties (Kubát 1985).

The study area

Distribution of *R. obtusifolius* in the Lužnice River floodplain, South Bohemia, Czech Republic, was studied in a narrow area, 0.1 to 1 km in width and 10 km in length, between the elevations 449 to 460 m a.s.l. The floodplain is bordered by terraces of Pleistocene origin, 1 to 5 m in height. Soil profiles of the floodplain are mostly complicated, with several layers of sand and loam formed during erosion-accumulation cycles (Chapters 2; 3.1). Experiments were carried out partly *in situ* and partly at a field station near the Lužnice village, 30 km north of the studied area, under partly controlled conditions.

Variation of *R. obtusifolius* and its distribution in the studied area

According to Rechinger (1932) and Kubát (1990) *R. obtusifolius* is represented by three subspecies in southern Bohemia. The oceanic subspecies *obtusifolius* has large valves with long teeth, the continental subspecies *sylvestris* has small valves and small or missing teeth. *R. *transiens* is characterised by having a morphology transitional between *R. *obtusifolius* and *R. *sylvestris*. Its geographical distribution partly overlaps those of the other two subspecies. Variation in *R. obtusifolius* was observed to be markedly high in the study area. Both plants with large fruits bearing long teeth and a single tubercle, and plants with small fruits, hardly any teeth on its margin and three equal tubercles can be found. In many places transitional types are also frequent. The extreme morphotypes are identical with subspecies *obtusifolius* and subspecies *sylvestris*, respectively (Klimeš 1989). For mapping purposes, transitional types between *R. *obtusifolius* and *R. *sylvestris* were merged with *R. *sylvestris*. This was considered permissible as intermediate morphotypes were usually found together with *R. *sylvestris*.

The distribution of *R. *obtusifolius* and *R. *sylvestris* with transitional types was markedly different in the study area (Fig. 5.17). The first taxon was common on intensively managed grasslands in the north of the study area and locally in other parts of the floodplain, especially near the terraces where garbage is deposited and where agricultural machines enter the floodplain area. The other subspecies *sylvestris* with transitions was found nearly everywhere, usually at a lower abundance.

Summarising, the results of mapping indicate that *R. *obtusifolius* prevails on places where disturbance is associated with high nutrient levels, whereas *R. *sylvestris* prefers more natural grasslands. *R. *sylvestris* tolerates competition from other tall herb species and a higher water level in contrast to *R. *obtusifolius*. Therefore, the crucial factors determining differences in distribution of *R. *obtusifolius* and *R. *sylvestris* in the study area are presumably nutrient levels associated with disturbance and soil moisture.

Ecological differentiation in *R. obtusifolius* in the studied area

DECORANA, a multivariate method introduced by Hill & Gauch (1980), was used to identify the principal factors determining distribution of *R. obtusifolius* subspecies.

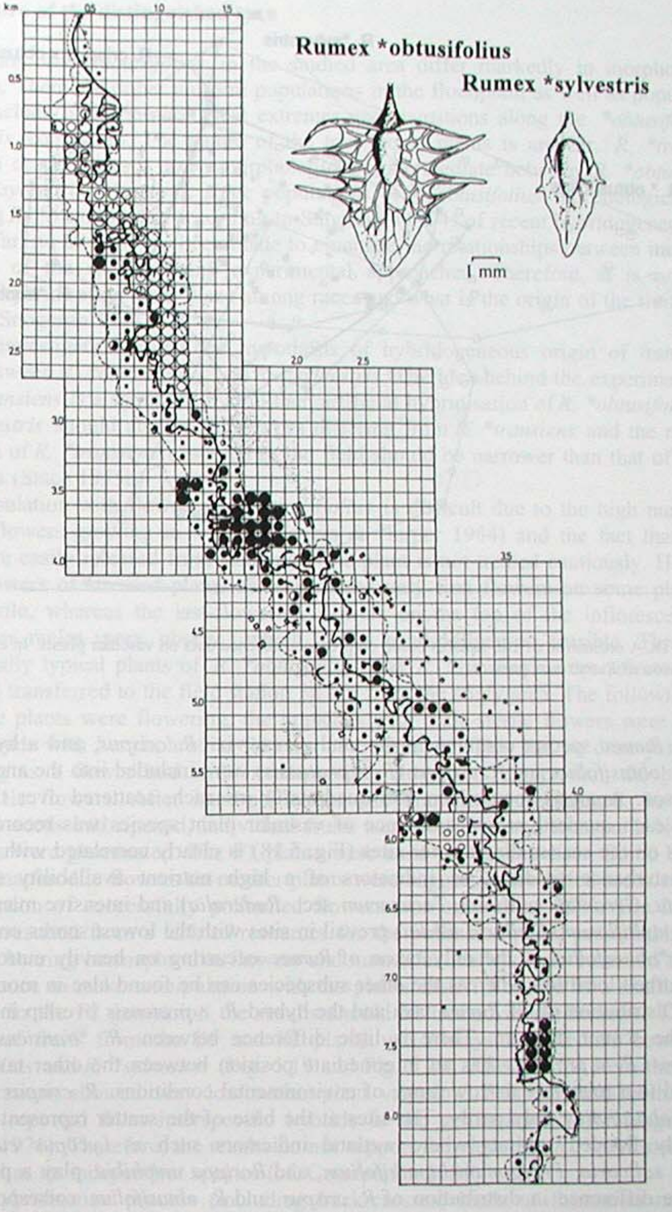

Fig. 5.17. Distribution of *R. *obtusifolius* (open circle) and *R. *sylvestris* (full circle) in the Lužnice River floodplain. *R. *sylvestris* includes transitional types as the transitional plants are usually mixed with *R. *sylvestris*. Size of a circle corresponds to the number of plants in a square (1 to 2, 3 to 9, 10 to 149, 150 to 499 and >500). The study area is delimited by a dashed line, woods are dotted, rectangles denote buildings. (after Klimeš 1989)

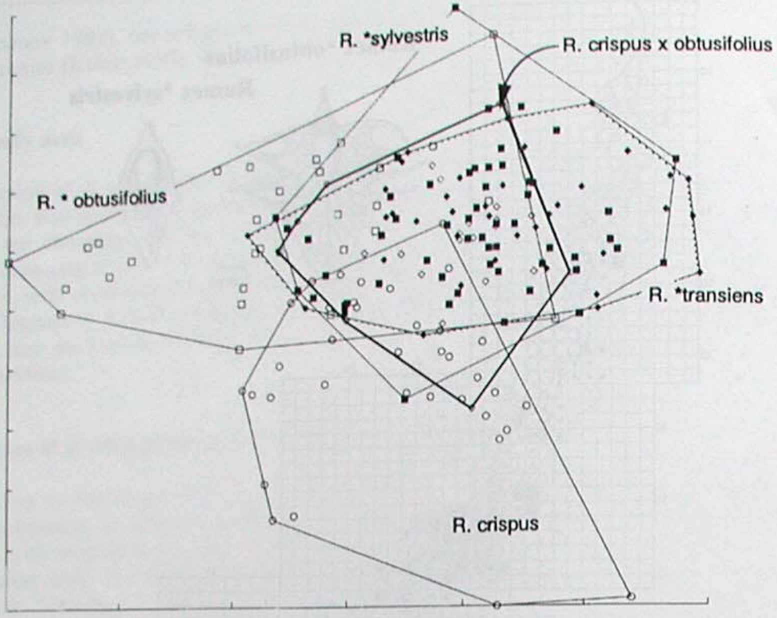

Fig. 5.18. DCA ordination of 186 squares based on presence/absence data on vascular plants. In each square a single taxon of *Rumex* was present.

Another *Rumex* species common in the study area, viz. *R. crispus*, and a hybrid between *R. obtusifolius* and *R. crispus* (*R.* × *pratensis*) were included into the analysis for comparison. Analysis focused on 186 quadrats, 1 m^2 each, scattered over the study area. In each quadrat, presence/absence of vascular plant species was recorded. The first axis on the scatter diagram for sites (Fig. 5.18) is clearly correlated with a fertilisation/disturbance gradient, as indicators of a high nutrient availability (*Dactylis glomerata, Geranium pusillum, Taraxacum* sect. *Ruderalia*) and intensive management (*Lolium multiflorum, Stellaria media*) prevail in sites with the lowest scores on the first axis. *R. *obtusifolius* is the only taxon of *Rumex* occurring on heavily eutrophicated and disturbed localities whereas the other subspecies can be found also in more natural stands. Distribution of all *Rumex* taxa and the hybrid *R.* × *pratensis* overlap in the centre of the scatter diagram. There is little difference between *R. *transiens* and *R. *sylvestris*. *R.* × *pratensis* has an intermediate position between the other taxa and is restricted to a relatively narrow range of environmental conditions. *R. crispus* overlaps with *R. obtusifolius* only partly. The sites at the base of the scatter represent wet and frequently flooded habitats where wetland indicators such as *Lycopus europaeus, Lythrum salicaria, Polygonum lapathifolium*, and *Rorippa amphibia* play a prominent role. The difference in distribution of *R. crispus* and *R. obtusifolius* corresponds to a better tolerance to higher water levels in the former species (Laan *et al.* 1989 a,b)

The nature of the distinguished taxa

Populations of *R. obtusifolius* in the studied area differ markedly in morphological variation. There are rather uniform populations in the floodplain as well as populations which include both morphological extremes and transitions along the **obtusifolius* – **sylvestris* continuum. The nature of the transitional plants is unclear. *R. *transiens* has been described as a taxon morphologically intermediate between *R. *obtusifolius* and *R. *sylvestris*. However, some populations of *R. obtusifolius* morphologically resembling *R. *transiens* are according to Snogerup (1994) of recent hybridogeneous origin. So far, no attempt has been made to elucidate the relationships between individual varieties of the species using experimental approaches. Therefore, it is not clear whether hybridisation takes place among races and what is the origin of the transitional variety (Snogerup 1994).

This investigation tested the hypothesis of hybridogeneous origin of transitional types between *R. *obtusifolius* and *R. *sylvestris*. The idea behind the experiment was: If *R. *transiens* is a stabilised hybrid then artificial hybridisation of *R. *obtusifolius* and *R. *sylvestris* should also produce types differing from *R. *transiens* and the range of variation of *R. *transiens* observed in the field should be narrower than that of F1 and F2 plants (Stace 1975b).

Manipulation with flowers of *R. obtusifolius* is difficult due to the high number of minute flowers growing in whorls (Cavers & Harper 1964) and the fact that pollen grains are easily released from stamens if the plant is not treated cautiously. However, some flowers of stressed plants as well as the very first flowers on some plants are male-sterile, whereas the last-flowering flowers on the top of the inflorescence are sometimes males (pers. observ.) which makes hand-pollination feasible. Three morphologically typical plants of *R. *obtusifolius* and *R. *sylvestris* were selected in the field and transferred to the field station 30 km from the study area. The following year, when the plants were flowering, the branches with male-sterile flowers were isolated and all buds with hermaphrodite flowers were removed. This can be done just before flowering as a flower bud with hermaphrodite flowers is bigger than the bud with male-sterile flowers. After hand-pollination the branches were bagged. In August, when the seeds had ripened, individual fruits were collected and measured. Next year the seeds were germinated. The F1 plants were used for back-crosses. Some branches with hermaphrodite flowers on mother plants were bagged to get selfed seeds.

Proportion of successfully pollinated flowers was only about 30%. The low seed outcome resulted from a lack of resources for the pollinated plant, presumably, as all branches bearing hermaphrodite flowers and numerous leaflets were removed from the inflorescence to make manipulation with the plants easier. Because of a small number of plants in the F2 generation the results should be treated as preliminary. The morphology of fruits from the F1 and F2 plants was always intermediate between *R. *obtusifolius* and *R. *sylvestris* (Fig. 5.19 and Fig. 5.20). The hybrids from the F1 and F2 generations showed very low within-plant variation. This contrasts with a great variation reported from interspecific hybrids in the genus *Rumex* (Rechinger 1964; Reichert 1971). Therefore, the results do not support the view that *R. *sylvestris* should be treated as an independent species (cf. Czerepanov 1981).

The hybridisation process (including back-crosses) leads to formation of hybrid swarms which cover the whole range of variability between *R. *obtusifolius* and *R. *sylvestris*. In the field a similar pattern was found: morphologically extreme *R. *obtusifolius* and *R. *sylvestris* plants were linked with plants having transitional morphology. They covered the whole gap between the two subspecies. As the

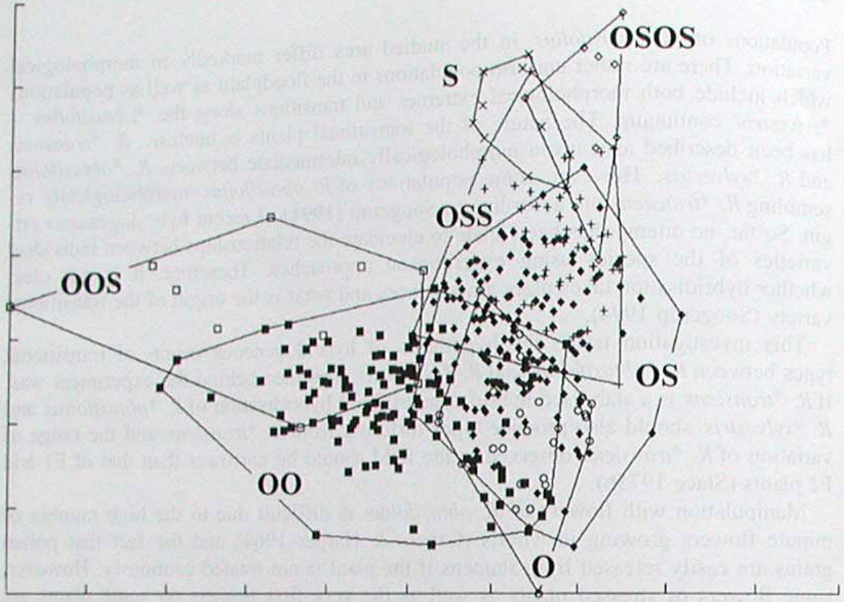

Fig. 5.19. DCA ordination of *R. obtusifolius* fruits. O – *R. *obtusifolius*, S – *R. *sylvestris*. OO – selfed seeds of *R. *obtusifolius*, OS – *R. *obtusifolius* × *R. *sylvestris*, OSS – backcross of *R. *sylvestris* × *R. *obtusifolius* with *R. *sylvestris*, OSOS – OS × OS, OOS – backcross of *R. *obtusifolius* × *R. *sylvestris* with *R. *obtusifolius*. Each point represents a single fruit. The input values were 25 variables. 10 fruits were measured per plant.

hybridogeneous plants were fully fertile, the process of hybridisation may result in extinction of the mother taxa. The consequence of this process is inevitable: on numerous localities in central Europe most specimens of *R. obtusifolius* cannot be assigned to either *R. *obtusifolius* or *R. *sylvestris*.

The results cannot reject a hypothesis suggesting that *R. *transiens* is a stabilised taxon of hybridogeneous origin. However, the contemporary hybridisation process between *R. *obtusifolius* and *R. *sylvestris* is likely a frequent phenomenon whenever the mother taxa meet together. Therefore, the transitional populations of *R. obtusifolius* may include both hybrid swarms and *R. *transiens*. The nature of *R. *transiens* requires further examination.

To conclude, the results of artificial hybridisation showed that F1 plants are fertile and capable of back-crosses. A wide range of variation was produced in this way, corresponding to the situation found in the field. The results confirm the view of Snogerup (1994) who believes that at least some transitional plants of *R. obtusifolius* are products of a recent hybridisation process.

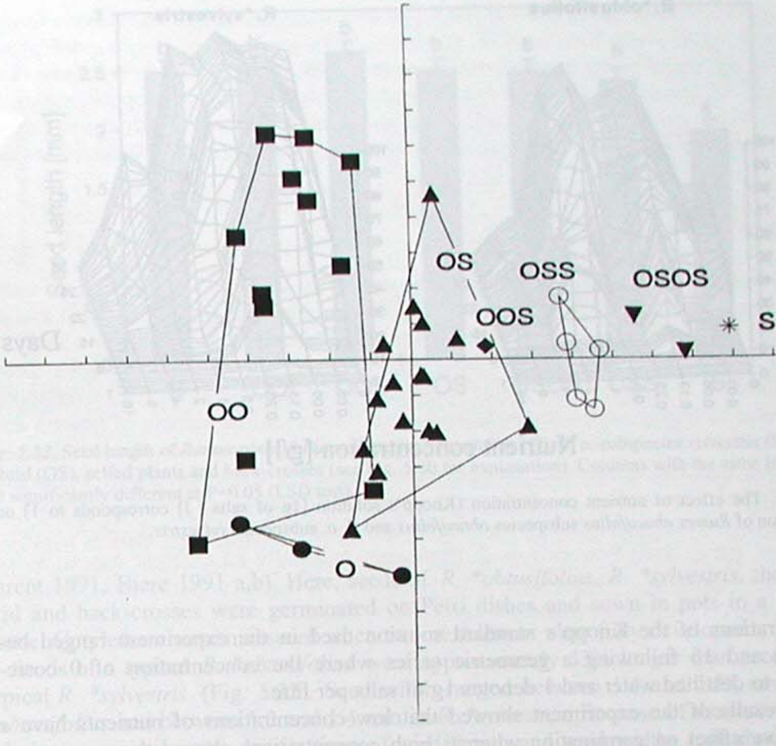

Fig. 5.20. DCA ordination of *R. obtusifolius* fruits. O – *R. *obtusifolius*, S – *R. *sylvestris*. OO – selfed seeds of *R. *obtusifolius*, OS – *R. *obtusifolius* × *R. *sylvestris*, OSS – backcross of *R. *sylvestris* × *R. *obtusifolius* with *R. *sylvestris*, OSOS – OS × OS, OOS – backcross of *R. *obtusifolius* × *R. *sylvestris* with *R. *obtusifolius*. Each point represents a single plant. Mean values were calculated for 25 variables and for individual plants using 10 fruits per plant.

Ontogenesis and phenology

Germination under different nutrient concentrations

There is an extensive literature on germination of *R. obtusifolius* (e.g. Cavers & Harper 1964; Hand *et al.* 1982; Takaki *et al.* 1985; Kendrick & Heeringa 1986; van Assche & Vanlerberghe 1989). However, as far as I am aware, there is no published data on differences between subspecies. Germination of both subspecies is very successful under optimum conditions. Under full light and at 20°C average temperature, 90 to 95% of seeds of both subspecies germinate within 3 days to 2 weeks (Klimeš, unpubl.). If the seeds are shaded or temperature is suboptimal, germination percentage decreases (e.g. Kendrick & Heeringa 1986). Germination in meadows which are often heavily fertilised is affected by local concentration of nutrients. The extremely high nutrient concentration is sometimes even toxic to meadow plants. The effect of nutrient concentration on germination of *R. obtusifolius* was tested using Petri dishes in the laboratory.

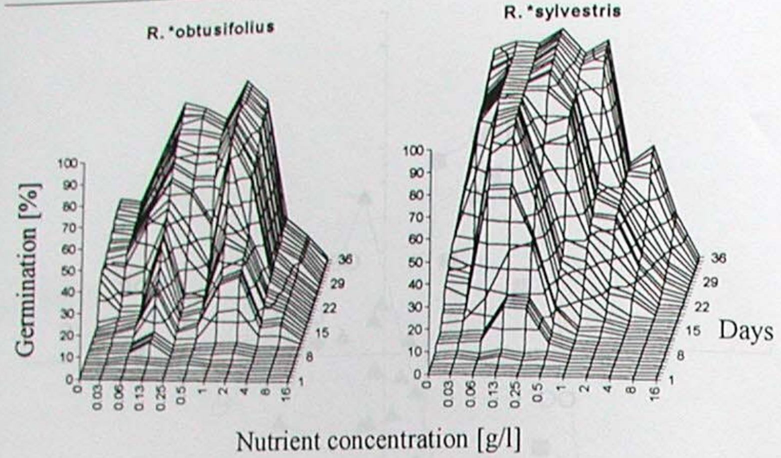

Fig. 5.21. The effect of nutrient concentration (Knopp's solution [1g of salts / l] corresponds to 1) on germination of *Rumex obtusifolius* subspecies *obtusifolius* and *R. o.* subspecies *sylvestris*.

Concentrations of the Knopp's standard solution used in the experiment ranged between 0 and 16 following a geometric series where the concentration of 0 corresponded to destilled water and 1 denotes 1g of salts per litre.

The results of the experiment showed that low concentrations of nutrients have a stimulative effect on germination whereas high concentrations slowed down germination and decreased the proportion of germinating seeds (Fig. 5.21). Germination of seeds of both subspecies started at 0.25 and 0.13 concentrations (Fig. 5.21). The highest proportion of germinating seeds was observed at higher concentrations, at about 1. Germination at high concentrations of nutrients was faster in *R. *sylvestris* than in *R. *obtusifolius*. At lower concentrations a higher proportion of germinating seeds was found in *R. *sylvestris* than in *R. *obtusifolius*. Both subspecies germinate at low concentrations of nutrients, however, germination of *R. *sylvestris* (the subspecies colonising more natural habitats) is faster.

The effect of most ions in the soil solution on seed germination is generally insignificant. However, there are two notable exceptions – nitrate and calcium – which stimulate germination, especially in light-requiring plants (Koller 1972). The presented results show that the effect of nutrient solution is very significant and even a small change in concentration causes a large effect. The differences between subspecies in their response to nutrient solution concentrations correspond to their distribution in the field. *R. *obtusifolius* prevails on regularly fertilised localities where a high nutrient concentration can be expected and where the other subspecies is almost missing.

Seed and cotyledon size

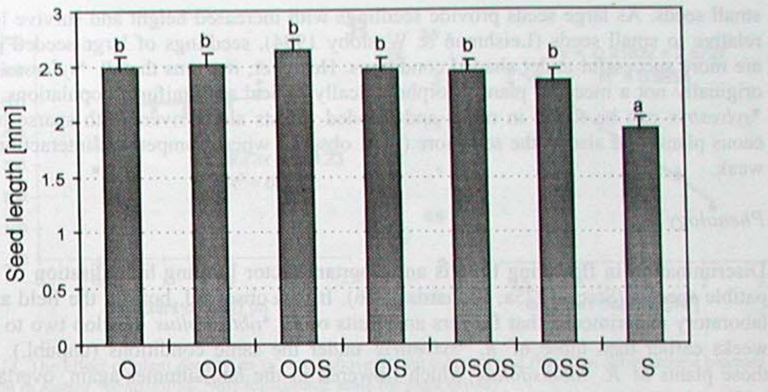

Fig. 5.22. Seed length of *Rumex obtusifolius* subspecies *obtusifolius* (O), *R. o.* subspecies *sylvestris* (S), their hybrid (OS), selfed plants and back-crosses (see Fig. 5.20 for explanation). Columns with the same letter are not significantly different at P=0.05 (LSD test).

Seed size has a great effect on seedling performance. The larger the seeds are, the bigger are the seedlings and better is their survival rate (Gross 1984; Keddy & Constabel 1986; Piper 1986; Marshall 1986; Wulff 1986 a,b,c; Shipley & Peters 1990; Shipley & Parent 1991; Biere 1991 a,b). Here, seeds of *R. *obtusifolius*, *R. *sylvestris*, their hybrid and back-crosses were germinated on Petri dishes and sown in pots in a greenhouse. Cotyledons were measured when two next leaves were fully developed.

Seeds of a typical *R. *obtusifolius* were approximately 33% longer than seeds of a typical *R. *sylvestris* (Fig. 5.22). Seed width ranged between 1.4 and 1.85 mm in *R. *obtusifolius* and between 1.2 and 1.4 mm in *R. *sylvestris*. Because of the low within-subspecies variation, the distributions of seed length and seed widths (not shown) for *R. *obtusifolius* and *R. *sylvestris* did not overlap. Surprisingly, hybrids between the subspecies as well as their descendants and plants from back-crosses had large seeds, comparable in size to those of *R. *obtusifolius*.

Seedlings of *R. *obtusifolius* had wider cotyledons (mean = 3.08, SD = 0.28) than those of *R. *sylvestris* (mean = 1.38, SD = 0.18) and grew much faster. In older plants the difference diminished (see control plants in the experiment with alternating watertable, Table 5.5). However, the proportion of plants which flowered in the first season was much higher in *R. *obtusifolius* than in *R. *sylvestris*. There was a marked difference between subspecies with respect to seed and cotyledon size. To a large extent, this difference determined the growth of seedlings. Big seeds of *R. *obtusifolius* produced seedlings with large cotyledons whereas *R. *sylvestris* had small seeds and seedlings.

The effect of seed size on germination and growth of seedlings in *R. obtusifolius* has been studied by Cideciyan & Malloch (1982) who found a strong correlation. However, it is not clear to what extent taxonomic diversity of the material used in the study explains the observed variation in seed size and, consequently, growth of seedlings. Cideciyan & Malloch (1982) divided the seeds into three size classes (<1.2 mm, 1.2 to 1.4 mm, >1.4 mm) with sieves. Therefore their seed size corresponds approximately to seed width. Seeds of both subspecies used in this study were bigger than the smallest size class of seeds defined by Cideciyan & Malloch (1982). It seems that their populations included both subspecies and transient plants.

It is surprising that *R. *sylvestris* growing in closed-canopy vegetation produces small seeds. As large seeds provide seedlings with increased height and survive longer relative to small seeds (Leishman & Westoby 1994), seedlings of large-seeded plants are more successful under shaded conditions. However, it seems that *R. *sylvestris* was originally not a meadow plant. Morphologically typical and uniform populations of *R. *sylvestris* can be found in moist and flooded forests along rivers with sparse herbaceous plants and also at the sea shore (pers. observ.) where competitive interactions are weak.

Phenology

Discrimination in flowering time is an important factor limiting hybridisation of compatible species (Stace 1975a; Richards 1986). It was observed, both in the field and in laboratory experiments, that flowers and fruits of *R. *obtusifolius* develop two to three weeks earlier than those of *R. *sylvestris* under the same conditions (unpubl.). Only those plants of *R. *obtusifolius* which flowered in the late summer again, overlapped with period of stigma receptivity in *R. *sylvestris*. However, the number of flowers and seeds produced later in the season is much smaller than the number of seeds formed during the first run. Moreover, *R. *sylvestris* frequently colonises places which are partly shaded. The shading is a factor promoting discrimination of flowering periods of the two *Rumex* subspecies as the plants which are less illuminated develop slowly. Therefore, the delayed flowering in *R. *sylvestris* is usually an efficient way to avoid hybridisation with *R. *obtusifolius*. Flowering time divergence is the most common mechanism preventing inter-specific gene flow between related taxa (Levin 1971; Rathcke & Lacey 1985). Habitat differentiation is usually more frequent and more efficient (Hurlbert 1970; Rathcke & Lacey 1985). In *R. obtusifolius* habitat differentiation is a primary factor preventing hybridisation among subspecies in the Lužnice study area. In disturbed places, where the subspecies have come together in recent times, the difference in flowering time may play a significant role.

The effect of density on growth of *R. obtusifolius*

*Biomass and nutrient concentrations in R. *obtusifolius*

Individuals of *R. obtusifolius* are usually scattered in meadows. Stands with high densities can also be found, especially on disturbed sites. To examine the effect of stand density on growth, biomass allocation, vertical structure and nutrient utilisation in *R. obtusifolius* an experimental approach was devised in which chemical analyses of soils and plants were carried out in stands with different plant densities. Seedlings of *R. *obtusifolius* were planted in squares $1 m^2$ in size at densities of 3 to 121 plants/m^2, with three replicates. The experiment was carried out using a sandy soil which naturally has lower levels of nutrients that those required by *R. obtusifolius*. To correct this a standard NPK fertilisation was applied, comprising 5.0 g of nitrogen, 5.5 g of K_2O and 5.5 g of P_2O_5 per m^2. Soil analyses were carried out at the end of the experiment from a mixed sample taken from the uppermost 10 cm of the soil on the three plots replicating plant density. The experiment began at the end of April and finished at the beginning of July. All plants flowered and produced fruits. Harvested biomass was sorted into stems, leaves and fruits, dried and weighed.

The above-ground biomass of *R. *obtusifolius* was observed to be almost stable at densities of 5 and more plants/m^2 (Fig. 5.23a). Mean plant weight decreased linearly with logarithm of density (Fig. 5.23b). Vertical distribution of above-ground plant biomass differed markedly along the range of densities (Fig. 5.24). Tallest plants were recorded at medium densities. The height of the layer with the largest fraction of reproductive tissues increased with plant density from 60-80 cm to 80-100 cm. A difference in the phenology of plants was recorded: plants at low densities developed faster than those at higher densities. The basal leaves of plants at lower densities were often partly dry, whereas those on plants at higher densities were still green at the time of harvest. Biomass allocation to reproductive structures decreased with increasing density. The proportion of stem biomass slightly increased with density as well as the proportion of leaf biomass. The latter increased sharply at higher densities (Table 5.2).

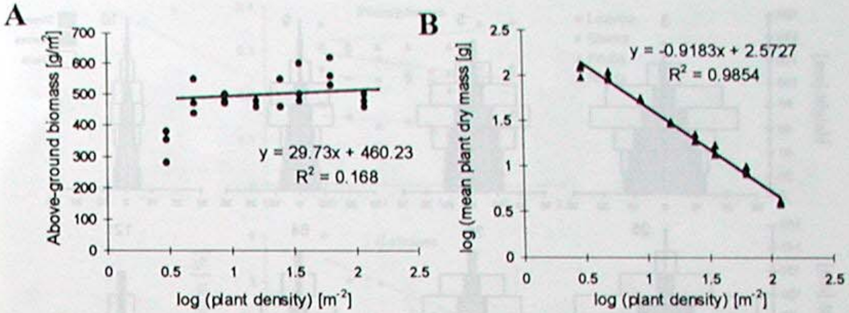

Fig. 5.23. The effect of plant density on (a) total aboveground biomass and (b) mean aboveground biomass per plant in *Rumex *obtusifolius*. Note logarithmic scale for plant density.

In spite of the fact that (except for the lowest density) aboveground biomass of the stand was approximately the same for all densities, concentration of basic nutrients in leaves, roots, stems and fruits differed among densities (Fig. 5.25). Potassium concentrations decreased with density in roots and fruits, while in stems and leaves it was density-independent. Calcium concentration in leaves and roots decreased markedly with stand density. However, there was no trend for stems and fruits. Finally, phosphorus concentrations were independent of plant density. Soil pH decreased slowly but significantly with plant density. Concentrations of potassium in the soil increased with plant density, a trend which corresponded to the decreasing potassium concentrations in roots and fruits as stand biomass was approximately the same for densities or five or more plants/m^2. Similarly, non-significant changes in phosphorus concentrations in soil along the plant density gradient corresponded with concentrations of phosphorus in plants which were independent of density (except for roots which comprised a smaller fraction of the total plant biomass – Fig. 5.26). Biomass allocation to stems indicates a mechanical strength of a plant (Niklas 1994). In dense stands an increase in plant height caused by etiolation was not matched by an increase in allocation to stems. As a consequence, the plants is weaker and may break. Thus an increase of mortality can be expected (Ogden 1970; Hutchings & Barkham 1976). In *R. obtusifolius* a different pattern was observed. The tallest plants were those at intermediate densities and biomass allocation to stems increased with density. This increase was at the expense of fruit production which decreased markedly with plant density.

To conclude, maximum above-ground biomass of *R. *obtusifolius* monocultures

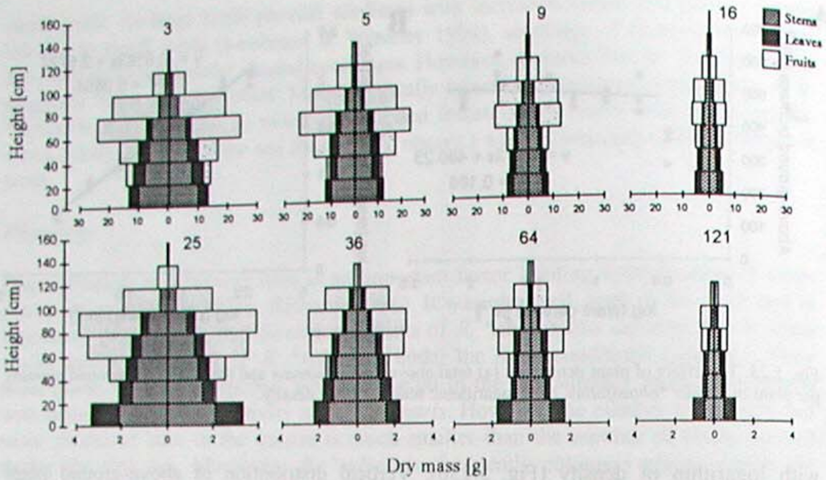

Fig. 5.24. The effect of plant density on vertical distribution of aboveground biomass in *Rumex *obtusifolius*.

Table 5.2. The effect of plant density on biomass allocation to fruits, stems and leaves of *Rumex *obtusifolius*, expressed as biomass of a particular organ * 100/above-ground biomass.

Density/m^2	3	5	9	16	25	36	64	121
Reproductive effort (%)	48.7	48.0	47.0	41.6	39.4	34.8	38.9	27.5
Allocation to stems (%)	37.7	37.8	39.8	41.5	41.8	44.6	40.2	42.6
Allocation to leaves (%)	13.2	13.1	11.7	14.7	16.1	19.3	19.2	29.7

(500 g of dry mass per m^2) was attained at densities of about 5 plants per m^2. This value is lower than those for total aboveground biomass in most meadow types in the Lužnice study area which is dominated by, among others, *Alopecurus pratensis*, *Deschampsia cespitosa* and *Phalaris arundinacea* (Tetter *et al.* 1988; Chapter 6.1). Unfortunately, no data have been published for stands dominated by non-graminoid species (but see Chapter 6.1). Plants at higher densities invested more biomass into higher strata and leaves, and were phenologically delayed. Plants at lower densities accumulated calcium (except fruits), potassium (roots and fruits) and phosphorus (roots) more than plants growing at higher densities.

*Reproductive allocation and phenology of R. *obtusifolius and R.*sylvestris along a density gradient*

A one-season experiment examined a narrower range of densities than the preceding experiment using rectangular plots (0.5 m^2) in a container. The range of densities used was 4, 8, 18 and 30 plants/m^2. Both subspecies (i.e. *R. *obtusifolius* and *R. *sylvestris*) were planted in monocultures with three replicates. The level of fertilisation applied was the same as in the preceding experiment. At the end of the experiment at the beginning of July, a large number of plants remained sterile because the experiment began too late in the season (in the beginning of May). The proportion of sterile plants increased with plant density and more plants of *R. *sylvestris* failed to flower than of *R. *obtusifolius* at any density (Table 5.3). Above-ground biomass of *R. *obtusifolius* was lower than that of *R. *sylvestris*, except for the highest density (Fig. 5.27). If only plants with generative organs are considered, the results still show the same trend but the differences for the highest density become non-significant. Reproductive effort (biomass of fruits/aboveground biomass) decreased with increasing density in both subspecies (Fig. 5.27c). If only fruiting plants are considered, the trend ceases in *R. *sylvestris* but is still significant in *R. *obtusifolius* (Fig. 5.27d). Therefore, small fertile plants of *R. *obtusifolius* allocated less biomass to reproduction than small plants of *R. *sylvestris*. In large plants no difference was found.

Biomass of fruits was closely related to biomass of stems and leaves in fertile plants of both subspecies (Fig. 5.28). The slope of the line, describing the relationship between dry mass of fruits and dry mass of stems+leaves was the same in both subspecies ($t = 0.019$, $P > 0.05$). However, the increment of the line was significantly higher in *R. *sylvestris* than in *R. *obtusifolius* ($t = 6.5$, $P < 0.01$). This means that the minimum

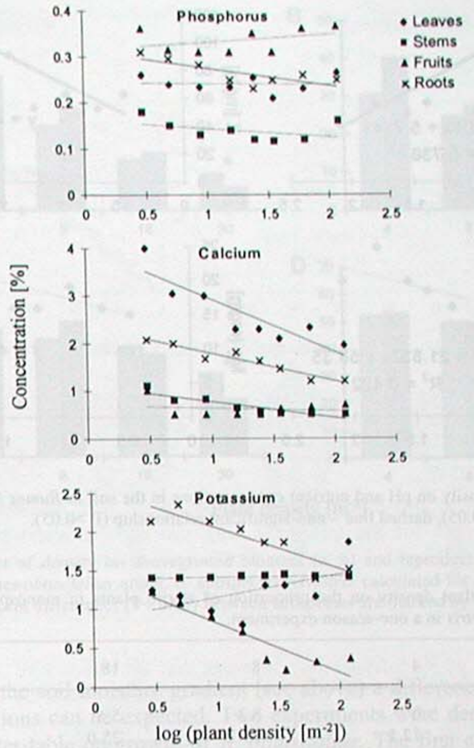

Fig. 5.25. The effect of plant density on nutrient cocentration in *Rumex *obtusifolius* tissues. Full line – significant ($P<0.05$), dashed line – non-significant relationship ($P >0.05$).

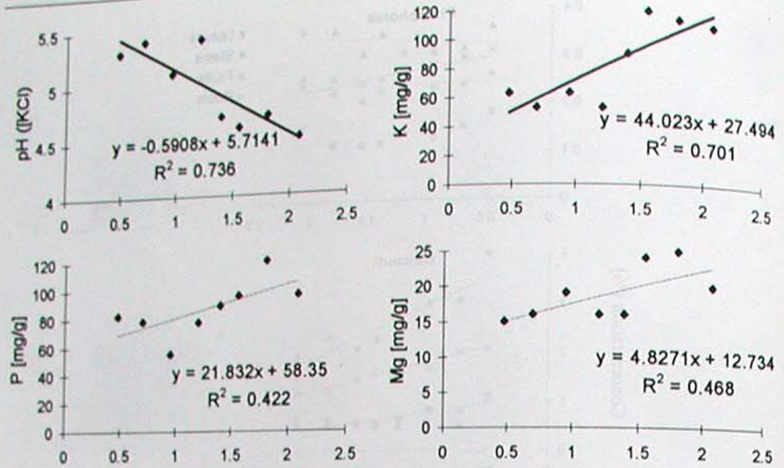

Fig. 5.26. The effect of density on pH and nutrient concentrations in the soil in *Rumex *obtusifolius* stands. Full line – significant ($P < 0.05$), dashed line – non-significant relationship ($P > 0.05$).

Table 5.3. The effect of plant density on the proportion of sterile plants in monospecific stands of *R. *obtusifolius* and *R. *sylvestris* in a one-season experiment.

Density/m^2	4	8	18	30
*R. *obtusifolius*	0	8.3	5.6	24.4
*R. *sylvestris*	12.5	33.3	25.0	55.0

biomass of stems and leaves needed for flowering was smaller in *R. *sylvestris* than in *R. *obtusifolius*. Biomass allocation to reproductive structures was studied in *R. crispus* by Hume & Cavers (1983). These authors found that reproductive allocation among populations sampled in different geographical regions was the same. *R. crispus* is a remarkably variable plant in Europe (Hume & Cavers 1982a,b; Akeroyd & Brigs 1983a,b) with several varieties occurring (Akeroyd 1988). The greatest differences in reproductive allocation between the studied types of *R. obtusifolius* relative to *R. crispus* populations correspond to a higher taxonomic level at which individual types of *R. obtusifolius* are recognised.

The effect of water-tables on *R. *obtusifolius* and *R. *sylvestris*

R. obtusifolius is a mesophillous plant, and therefore is poorly adapted to anaerobic soil conditions in flooded areas (Laan *et al.* 1989a). If a period of flooding/waterlogging is short, older roots decay (being replaced by adventitious roots) and growth rate decreases (Laan *et al.* 1989a,b). Longer periods with floods may result in a decrease of fertility, and eventually in mortality of the plants not adapted to these conditions (Blom *et al.* 1990). As the studied subspecies of *R. obtusifolius* have different distributions along the soil moisture gradient (see above) a difference in their tolerance to anaerobic conditions can be expected. Two experiments were designed in order to test the effect of water-table on growth of *R. obtusifolius*. The first experiment studied the effect of a stable water table on growth and biomass allocation in *R. *obtusifolius*. The second studied the effect of floods with different duration and timing on growth of *R. *sylvestris* and *R. *obtusifolius* using alternating waterlogged and mesic conditions.

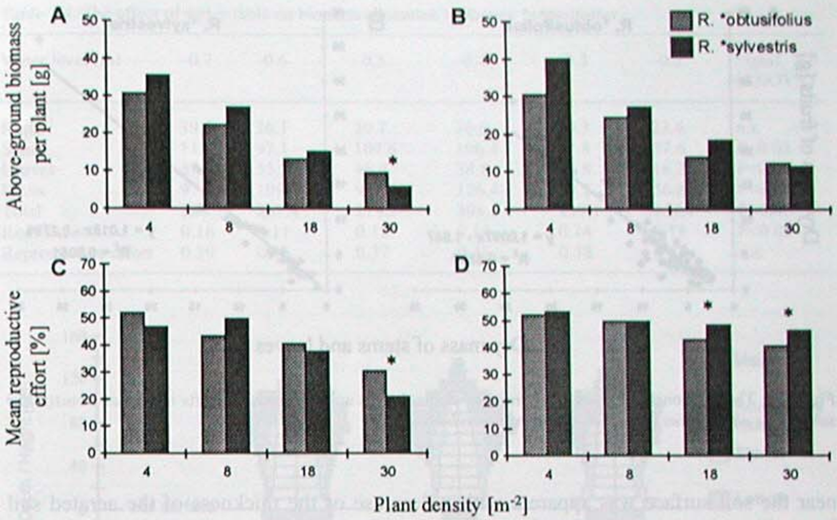

Fig. 5.27. The effect of density on aboveground biomass (a, b) and reproductive effort (c, d) in *Rumex obtusifolius* subspecies *obtusifolius* and *R. o.* subspecies *sylvestris* calculated for all plants (a, c) and fertile plants (b, d). Significant differences ($P < 0.05$) between subspecies are marked by asterisk.

*The effect of different water-tables on biomass of R. *obtusifolius*

At the beginning of May, seedlings of *R. *obtusifolius* were planted in containers filled with a sandy soil at a density of 32 plants/m^2. Six levels of water-table ranging from –20 to –70 cm were used. The rectangular plots were 0.5 m^2 in size and three replicates were used. Aboveground biomass of individual *Rumex* specimens was harvested at the end of June. Total root biomass was estimated for each plot. The roots were washed out on a 1 mm sieve and divided into two fractions with root diameter less than and more than 1 mm. The biomass was dried at 90°C and weighed.

The only treatment which differed from the others was that of the highest water-table (Table 5.4). Plants grown at other water levels had approximately the same aboveground biomass, belowground biomass and total biomass. There was no difference in reproductive effort at all. Root/shoot ratio increased with increasing water-table but root biomass was independent of it. Vertical distribution of biomass was markedly affected in the belowground fraction by water-table level (Fig. 5.29). Only a small fraction of roots penetrated in the anaerobic environment below the water-table at any level of water-table. Accumulation of roots (especially thin roots) in the soil horizons

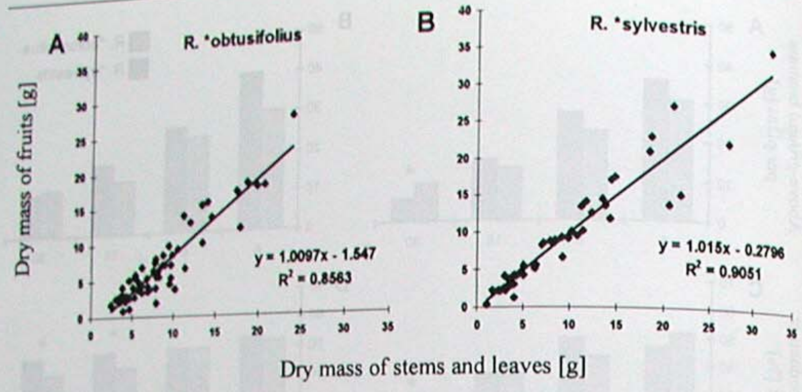

Fig. 5.28. The relationship between dry mass of stems+leaves and dry mass of fruits in *Rumex obtusifolius* subspecies *obtusifolius* (a) and *R. o.* subspecies *sylvestris* (b).

near the soil surface was apparent with a decrease of the thickness of the aerated soil layer. In contrast, except for the treatment with the highest water-table (Fig. 5.29), there was hardly any difference in vertical distribution of aboveground biomass. If the soil was not flooded *R. *obtusifolius* plants utilised nutrients from the whole soil profile. They hardly penetrated or survived in the anaerobic environment below the water-table however.

The rooting pattern of *R. *obtusifolius* suggests that the absence of the subspecies in tall herbaceous vegetation along the Lužnice River may be caused by its intolerance to the high water-table (cf. Voesenek & Blom 1987). From this experiment it may be concluded that *R. obtusifolius* may tolerate a stable water level as high as 30 cm below the soil surface without apparent difficulties. Roots accumulate in the upper soil horizon at higher water levels, however, their total amount is not affected. In the aboveground biomass, the effect of increasing water level becomes significant if less than 30 cm of aerated soil is available.

*The effect of water regime alteration on R. *obtusifolius and R. *sylvestris*

Seeds of both subspecies were collected in September 1988. The germination test was started in the middle of April 13 1989, by placing seeds on moist filter paper in Petri dishes, and was carried out at room temperature. After two weeks, seedlings of both subspecies (altogether 320 individuals) were planted in pots, 10 × 10 × 15 cm in size, filled by a nutrient-poor substrate (a mixture of sand and loam) and kept in mesic, freely drained conditions (mesic environment). After nine days a randomly chosen half of pots were waterlogged in a container (waterlogged environment). The water regime was then alternated in one half of the randomly chosen pots in all treatments again on Days 22, 44 and 68 so that 8 treatments differing in their history of water regime arose at the end (Day 101). This arrangement resulted in different lengths of waterlogging periods which started at a different age of the plants studied. At the end of each period eight plants (after the last period only six plants remained) were randomly selected from each treatment, the leaf area of their leaves was measured (except for the last period) and after that, plant biomass was separated into three categories – laminae, petioles and roots – dried at 90°C and weighed. The differences between subspecies were significant in most biomass and allocation parameters (Table 5.5a). Plants of *R. *obtusifolius* were bigger, produced more leaves and had greater biomass. The effect of waterlogging on total biomass and its components was non-significant in young plants except for laminae (Table 5.5b), whereas later it became highly significant (Table 5.5c). In contrast, the effect of subspecies identity on total biomass and its components was very marked in the first harvest (Table 5.5a) and then disappeared, except for aboveground biomass and laminae (Table 5.5c). The differences in aboveground biomass and its components were non-significant among treatments with *R. *obtusifolius*, except for laminae, petioles and aboveground biomass in older plants. Differences in belowground and total biomass emerged in the third harvest (Table 5.5c). *R.*

Table 5.4. The effect of water-table on biomass allocation in *Rumex *obtusifolius.*

Water level (m)	–0.7	–0.6	–0.5	–0.4	–0.3	–0.2	Signif. (ANOVA)
Roots	39.5	26.1	30.7	36.9	29.3	23.6	n.s.
Stems	115.0	97.1	109.6	106.4	97.8	57.6	P<0.05
Leaves	37.2	35.2	46.4	38.8	32.8	16.2	P<0.05
Fruits	97.0	109.0	92.5	126.4	79.2	56.8	P<0.05
Total	288.7	267.4	279.2	308.5	239.1	154.1	P<0.05
Root/shoot	0.16	0.11	0.12	0.14	0.14	0.18	P<0.05
Reproductive effort	0.39	0.45	0.37	0.47	0.38	0.43	n.s.

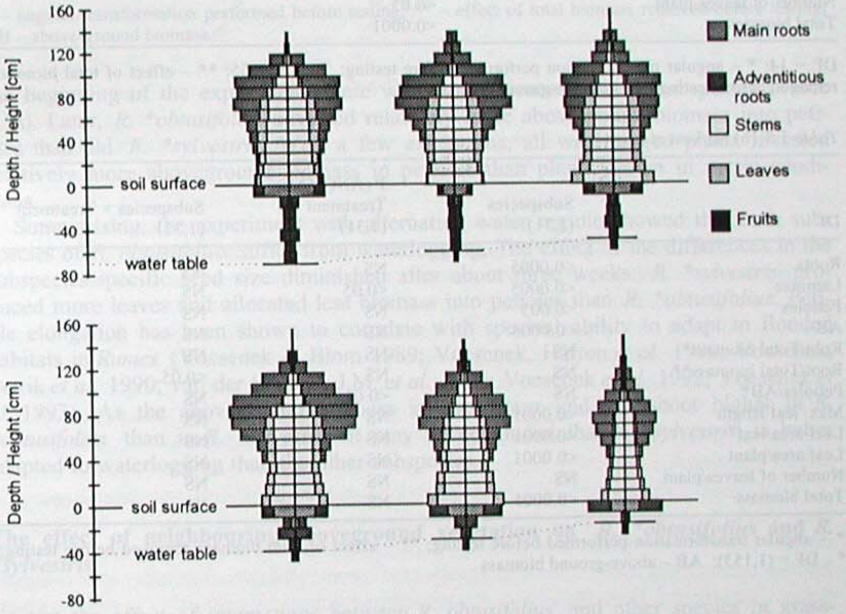

Fig. 5.29. The effect of water-table on vertical distribution of biomass in *Rumex *obtusifolius.*

Table 5.5. The effect of waterlogging on biomass allocation in two subspecies of _Rumex obtusifolius_.

Table 5.5. (a) Harvest at day 9.

	P (t-test)
Roots	<0.0001
Laminae	<0.001
Petioles	<0.0005
Above-ground biomass (AB)	<0.0005
Root/Total biomass*	<0.0005
Root/Total biomass**	NS
Petioles/AB*	NS
Maximum leaf length	<0.0001
Leaf area/leaf#	<0.0005
Leaf area/plant	<0.0005
Number of leaves/plant	<0.05
Total biomass	<0.0001

DF = 14; * – angular transformation performed before testing; # – DF = 55; ** – effect of total biomass removed before testing; AB – above-ground biomass

Table 5.5. (b) Harvest at day 44.

		P (ANOVA)	
DF	Subspecies (1,31)	Treatment (1,31)	Subspecies × Treatment (1,31)
Roots	<0.0005	NS	NS
Laminae	<0.0005	<0.05	NS
Petioles	<0.005	NS	NS
AB	<0.0005	NS	NS
Root/Total biomass*	NS	NS	NS
Root/Total biomass**	NS	NS	<0.05
Petioles/AB*	NS	<0.01	NS
Max. leaf length	<0.0001	NS	NS
Leaf area/leaf#	<0.0001	NS	NS
Leaf area/plant	<0.0001	NS	NS
Number of leaves/plant	NS	NS	NS
Total biomass	<0.0005	NS	NS

* – angular transformation performed before testing; ** – effect of total biomass removed before testing; # – DF = (1,153); AB – above-ground biomass

Table 5.5. (c) Harvest at day 101.

		P (ANOVA)	
DF	Subspecies (1,95)	Treatment (7,95)	Subspecies × Treatment (7,95)
Roots	NS	<0.0001	<0.0001
Laminae	<0.0005	<0.0001	<0.05
Petioles	NS	<0.01	<0.005
AB	<0.005	<0.0001	<0.01
Root/Total biomass*	<0.0001	<0.0001	<0.05
Root/Total biomass**	<0.0001	<0.0001	<0.05
Petioles/AB*	<0.0001	<0.0001	NS
Max. leaf length	<0.05	<0.0001	<0.05
Total biomass	NS	<0.0001	<0.0001

* – angular transformation performed before testing; ** – effect of total biomass removed before testing; AB – above-ground biomass

*sylvestris revealed a different response: there were no differences among treatments in the second harvest (Table 5.5b), whereas older plants subjected to an alternating water regime produced mostly more biomass (viz. total biomass and partly also roots and laminae) than the other ones. Leaf area (LA) per plant was higher in _R. *obtusifolius_ than in _R. *sylvestris_ in the youngest plants (Table 5.5a). Leaves of _R. *obtusifolius_ were larger than those of _R. *sylvestris_ in all treatments except for seedlings and older plants waterlogged repeatedly or for long periods (Table 5.5c). There was no difference among treatments in the mean LA of _R. *sylvestris_ leaves in contrast to the other subspecies. The number of leaves was related to the LA per plant and mean size of leaves per plant. _R. *obtusifolius_ had more leaves than _R. *sylvestris_ only during the first period (Table 5.5a). After day 44 however, more leaves were found in _R._ _*sylvestris_. There was a trend of decreasing number of leaves in waterlogged plants in both taxa. The biomass of petioles/aboveground biomass was independent both of total and aboveground biomass (r = –0.080 and –0.079; n = 320, P> 0.10 in both cases). At the beginning of the experiment, there was no difference between subspecies (Table 5.5a). Later, _R. *obtusifolius_ invested relatively more aboveground biomass into petioles than did _R. *sylvestris_. With a few exceptions, all waterlogged plants invested relatively more aboveground biomass in petioles than plants grown in mesic conditions.

Summarising, the experiment with alternating water regime showed that both subspecies of _R. obtusifolius_ suffer from waterlogging. The effect of the differences in the subspecies-specific seed size diminished after about three weeks. _R. *sylvestris_ produced more leaves and allocated less biomass into petioles than _R. *obtusifolius_. Petiole elongation has been shown to correlate with species' ability to adapt to flooded habitats in _Rumex_ (Voesenek & Blom 1989; Voesenek, Harren _et al._ 1990; Voesenek, Petrik _et al._ 1990; van der Sman A.J.M. _et al._ 1991; Voesenek _et al._ 1992; Voesenek _et al._ 1993). As the aboveground biomass is also lower and root/shoot higher in _R. *obtusifolius_ than in _R. *sylvestris_ it may be concluded that _R. *sylvestris_ is better adapted to waterlogging than the other subspecies.

The effect of neighbouring aboveground vegetation on _R. *obtusifolius_ and _R. *sylvestris_

To test the effect of interactions between _R. obtusifolius_ and other species in grasslands, a one-season experiment was carried out in the field at the study site on the Lužnice floodplain. Six localities were chosen, three of them with _R. *obtusifolius_ and three with _R. *sylvestris_. Twenty target _Rumex_ specimens were randomly selected on each locality and circular plots, 1 m in diameter, were fixed. Another ten randomly placed plots without _Rumex_ were established as controls. In 10 plots with _Rumex_ specimens, aboveground biomass of all species except _R. obtusifolius_ was removed. This was done three times: in the beginning of April, May and June on all the plots. The experimental plots were harvested in the end of June, before the meadows were mown. Aboveground biomass of target plants and all other species to a distance of 0.5 m was cut, dried and weighed.

There was a considerable difference in results between plots (Fig. 5.30). On the heavily fertilised plot (Plot 1), _R. *obtusifolius_ was strongly suppressed by neighbouring vegetation. On other plots the effect of neighbouring plants was much weaker and until some threshold value of biomass of neighbouring plants was reached growth of

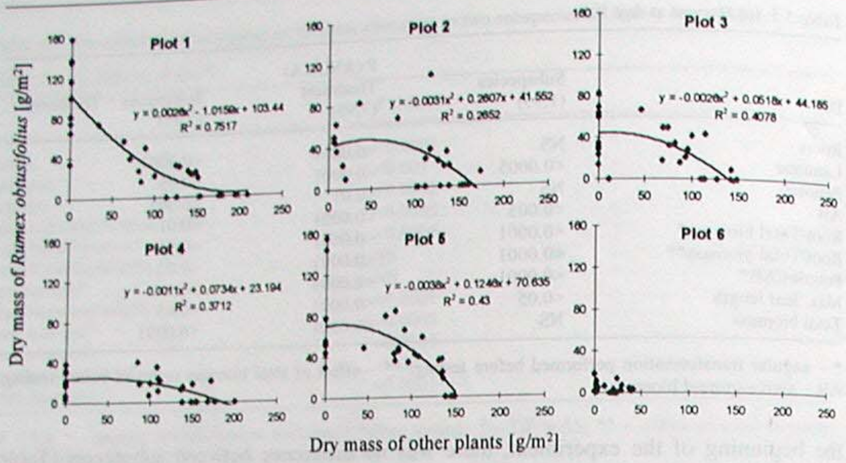

Fig. 5.30. The effect of neighbouring vegetation on aboveground biomass of *R. *obtusifolius* (Plots 1-3) and *R. *sylvestris* (Plots 4-6). Significant relationships are fitted by second order polynoms.

Rumex plants was not affected. On an old-field with a sparse vegetation dominated by *Poa pratensis* (Plot 6) no effect of intra-specific competition on *R. *sylvestris* was found. The other extreme was a wet meadow with *Phalaris arundinacea* (Plot 4) where biomass of *R. *sylvestris* was always low. This can be explained by the anaerobic soil conditions which are detrimental for *Rumex* (see above and Blom *et al.* 1990). In contrast to the other subspecies, *R. *sylvestris* could survive there, but its optimum is in more mesic conditions. In fertilised grasslands with a vigorous vegetation, *R. obtusifolius* was significantly suppressed by neighbouring vegetation. After surrounding vegetation was removed, it achieved an extremely high biomass in comparison with closed grasslands.

Jeangros & Nöberger (1992) found that *R. obtusifolius* is less sensitive to shading than other grassland species because of a greater increase in specific leaf area in shaded leaves. This adaptation may minimise the effect of the intense competition in tall herbaceous vegetation. Similar results were presented also for other broad-leaved docks (Haugland 1993). However, *R. obtusifolius* interacts with other meadow plants not only by competing for light and nutrients (Melzer *et al.* 1984). It may also release allelochemical agents suppressing germination and growth of other plants (Lutts *et al.* 1987; Carral *et al.* 1988). The results of the experiment suggest that the intensity of competition measured as a biomass response of the target plant is much higher in productive than in unproductive environments. This supports the view of Grime (1979; see also Grace 1991 for discussion) who claims that competition is less intense in unproductive habitats.

Competition between subspecies of *Rumex obtusifolius*

Most plants of *R. *obtusifolius* and *R. *sylvestris* grow at low densities in the study area. They come into contact rather infrequently, except for heavily disturbed areas with a high nutrient supply where density of *R. obtusifolius* may be relatively high. As it has been shown that demands for basic nutrients of the subspecies are not much different, competition between them could play a significant role. As the species prefer soils with a high nutrient content (Gebauer *et al.* 1984, Melzer *et al.* 1984), especially in nitrogen (Jeangros & Nöberger 1990), nutrient availability seems to be a factor which could potentially mediate competition between the two subspecies. To test this, a one-season experiment using a classical de Wit's arrangement was carried out. Sixteen plants of the respective subspecies were planted per m² in monocultures and mixed in other three treatments so that the total density of plants was kept constant. The plots were established on sandy soil where nutrient availability was too low to cover demands of *R. obtusifolius*. The plots were fertilised with three levels of nutrients: N1 – 1.6 g of nitrogen, 1.8 g of K_2O and 1.8 g of P_2O_5 per m², N2 – 5.0 g of nitrogen, 5.5 g of K_2O and 5.5 g of P_2O_5 per m² and N3 – 15.0 g of nitrogen, 16.5 g of K_2O and 16.5 g of P_2O_5 per m².

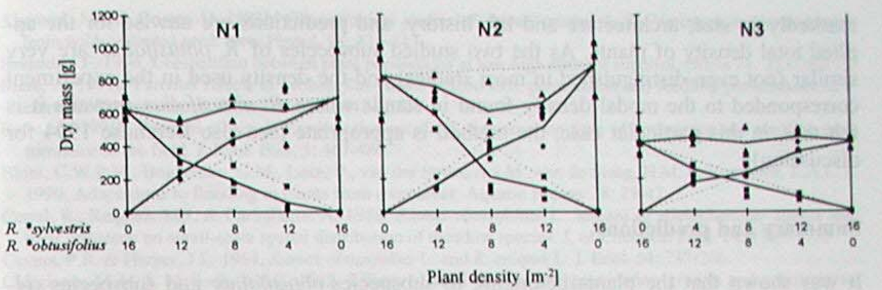

Fig. 5.31. De Wit's diagrams of competition between *R. *obtusifolius* and *R. *sylvestris*. N1, N2 and N3 denote fertilisation levels.

Total biomass of *Rumex* plants was the highest at N2 and lowest at N3, irrespective of the subspecies and subspecies mixtures (Fig. 5.31). Growth of individual subspecies differed between nutrient levels. Under the highest level (N3) the subspecies did not differ – they both suffered from the too-high nutrient concentration in the same way. *R. *obtusifolius* was suppressed at the lowest nutrient level (N1) whereas *R. *sylvestris* did not respond in any way. At the medium nutrient level (N2) where the highest biomass was obtained, total biomass was apparently lower for mixtures than for monocultures. This indicates a negative effect caused by allelopathy for example.

To summarise, the relationship between *R. *obtusifolius* and *R. *sylvestris* may vary in dependence of a particular nitrogen level. Under stressed conditions caused by toxic levels of nutrients, either no difference in growth between subspecies was found or *R. *obtusifolius* was weaker. Under optimum conditions plants of both subspecies showed a negative effect on each other. Under low nutrients *R. *obtusifolius* was suppressed by *R. *sylvestris.* At a growth stage of the young plants where they are unable to utilise water from deeper soil horizons, a mutualistic relationship (independent of subspecies identity) was observed (Klimeš, unpubl.). A shading of soil surface by leaves prevents drying out of the soil during sunny spring days. Therefore, the plants planted at higher densities do not suffer from a low water availability and grow better than those at lower densities.

The arrangement of the de Wit's competition experiments has been criticised (Jolliffe *et al.* 1984; Firbank & Watkinson 1985; Connolly 1986, 1987, 1988; Taylor & Aarssen 1989). The method is apparently not appropriate for pairs of plants differing markedly in size, architecture and life history, and predictions are unwise for the applied total density of plants. As the two studied subspecies of *R. obtusifolius* are very similar (not even distinguished in most studies) and the density used in the experiment corresponded to the modal density found in stands where *R. obtusifolius* prevails it is felt that, in this particular case, the method is appropriate (see also Berendse 1994 for discussion).

Summary and predictions

It was shown that the plants belonging to subspecies *obtusifolius* and subspecies *sylvestris* differ not only in morphology and local distribution but also in ontogenesis, phenology, density-dependence and tolerance to waterlogging. The results also indicate that the studied taxa represent well defined taxonomic units in the studied area. *R. *sylvestris* colonises more natural habitats than the other subspecies and is better adapted to competition, shading and high water levels. By contrast, *R. *obtusifolius* tolerates extremely high nutrient levels and its initial growth is faster than that of *R. *sylvestris*. It follows (i) from the analysis of the recent distribution of *Rumex* taxa along the Lužnice River and (ii) from results from the experiments carried out that *R. *obtusifolius* may invade new areas if fertilisation levels and disturbance by agricultural machines increases. A similar trend in spreading can be expected also in *R. *sylvestris*, but on more natural places only.

In the near future the two subspecies may come more frequently into contact where intensification of agricultural practices disturbing plant cover continues. A hybridisation between them may lead to prevalence of the transitional types on many places and local extinction of the typical *R. *obtusifolius* and *R. *sylvestris*. Flood frequency and duration is unpredictable in the study area both within and between years. After long periods of flooding *R. *obtusifolius* may retreat to some extent. However, because of the high amounts of *Rumex* diaspores available anywhere in the study area the local extinction will be probably compensated by new colonisations or by regeneration from seed bank.

If regular management ceases, both subspecies of *R. obtusifolius* will decrease in abundance. This is because of two principal factors. First, an invasion of tall competitive herbs (*Urtica dioica, Phalaris arundinacea*) shading other plants can be expected. They suppress most of the meadow plants including *Rumex* species. The second reason is probably even more important: accumulation of litter in unmown meadows prevents germination of *R. obtusifolius* seeds. Thus, ageing of *Rumex* populations can be expected which may later result in a decline or local extinction of the species. As *R. *sylvestris* tolerates better competition from the other species its persistence in uncut meadows may be longer than that of *R. *obtusifolius*.

Acknowledgements

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