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Effect of nitrogen, phosphorus and potassium availability on mother plant size, seed production and germination ability of *Rumex crispus*

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Summary

Rumex crispus is believed to be a highly nutrient-demanding weedy species that spreads mainly by seeds. However, the effects of nutrient availability on its performance and seed production have never been fully investigated. In this study, we investigated how plant size, seed production and germination were affected by the supply of N, P and K. In May 2008, a pot N, P and K fertiliser experiment was established in Prague (Czech Republic). During 2009, plant growth data were collected, and fully ripe seeds were tested for germination and N, P and K concentrations. *Rumex crispus* showed high phenotypic plasticity in plant height, number of leaves, leaf length and number of stems per plant in relation to N, P and K supply. Seed production per plant ranged from <2000 in the control and low P treatment up to almost 25 000 in the high NPK treatment. More than 16 000 seeds were produced per plant in all treatments where N and P were applied together. To produce a high quantity of rapidly germinating seeds, *R. crispus* requires a balanced N, P and K supply, as a deficiency of P and K together with a high N supply can result in the production of P- and K-deficient seeds (P and K <3 g kg^{-1}) with lower germination ability. In central Europe, at least some populations of *R. crispus* do not flower in the seeding year and are strictly monocarpic. Given the short lifespan and monocarpic character of the species, control is probably most effective if applied at the rosette stage, prior to the production of viable seeds.

Keywords: curled dock, germination, maternal nutrient effect, monocarpic biennial, phenotypic plasticity, plant nutrition.

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Introduction

Rumex crispus L. (curled dock) is native in temperate Europe and today is a widely distributed weed species around the world (Cavers & Harper, 1964; Zaller, 2004). Thus, it is frequently studied in many countries. Using *R. crispus* or curled dock as a keyword in a search in the Web of Science database (http://apps.isiknowledge.com) retrieved 546 records (129 with *R. crispus* directly in the title) from 1945 to November 2011. The majority of these studies were connected with the control of *R. crispus* on agricultural land (Hatcher, 1996; Zaller, 2004; Dimitrova & Marinov-Sarafimov, 2008), the germination ecology of seeds (Cavers & Harper, 1966; Totterdell & Roberts, 1979; Baskin & Baskin, 1985; Pye & Andersson, 2009) and recently its medicinal use (Coruh *et al.*, 2008). *Rumex crispus* is a highly variable species that is particularly abundant in cultivated fields,

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wasteland, demolition sites, riverbanks and along roadsides (Weaver & Cavers, 1979; Grime *et al*., 1988).

Grime *et al*. (1988) described *R. crispus* as a short-lived perennial or, more rarely, as an annual herb that is able to flower in its seeding year. *Rumex crispus* often dies after flowering and tends to disappear from permanent grassland if new seedlings fail to establish (Bond *et al*., 2007). Perennation of *R. crispus* can be supported by cutting before flowering, although *R. crispus* is generally much more negatively affected by severe defoliation than *Rumex obtusifolius* L. (broad-leaved dock) (Bentley & Whittaker, 1979; Hongo, 1989). According to Hume and Cavers (1983a), plants of *R. crispus* do not flower in the seeding year in North America, unlike in Britain and the rest of Europe. Nevertheless, in Central Europe (Prague, Czech Republic), no flowering of *R. crispus* was documented in the seeding year under optimal growth conditions (Křišťálová *et al*., 2011). Likewise, Hongo (1989) recorded no flowering of *R. crispus* in the seeding year in the cold winter region of Hokkaido (Japan). Further research is therefore required to adequately describe the flowering behaviour of *R. crispus*.

Although many related studies have been conducted, the effect of nutrient availability on the phenotypic plasticity of *R. crispus* has rarely been investigated. According to Jursík *et al*. (2008), *R. crispus* is generally believed to be nitrophilous, but it probably has lower nitrogen (N) requirements than *R. obtusifolius*. In a similar manner to *R. obtusifolius* (Humphreys *et al*., 1999; Hiltbrunner *et al*., 2008; Strnad *et al*., 2010), soils rich in phosphorus (P) and potassium (K) are probably more favourable for *R. crispus* growth than P- and K-poor soils, but detailed experimental data are missing. Furthermore, to the best of our knowledge, no study has investigated how the growth, plant longevity and seed production of *R. crispus* are affected by nutrient availability. Such information is only available for the related weedy species *R. obtusifolius* (Hrdličková *et al*., 2011).

Estimates of seed production and the weight of achenes in *R. crispus* are highly variable, ranging from 100 to over 40 000 achenes per individual plant and from 0.7 to 2 g per 1000 achenes (Cavers & Harper, 1964, 1966). In a study of 11 different *R. crispus* populations, seed production per individual plant ranged from 13 700 to 28 300, and the weight of 1000 achenes without perianths ranged from 1.25 to 1.72 g in ideal garden conditions (Hume & Cavers, 1983b). Bentley *et al*. (1980) recorded 2400 to 3900 seeds produced per individual plant and a 1000 seed weight ranging from 1.45 to 1.9 g. It is well known from grain crops that the nutritional status of the mother plant affects the chemical composition of seeds, particularly the N concentration (Acreche & Slafer, 2009). This maternal nutrient effect can affect seed germination and the subsequent performance of offspring, as documented for *R. obtusifolius* (Hrdličková *et al*., 2011), several *Plantago* species (Miao *et al*., 1991; Latzel *et al*., 2009), *Chenopodium album* L. (Wulff *et al*., 1999) and *Pisum sativum* L. (Amjad *et al*., 2004). However, no study has been performed to investigate the effect of the nutritional status of the mother plant on seed production per individual plant of *R. crispus*, on seed weight, seed chemical properties or germination. The results of such a study would help to identify the optimal N, P and K availability in the soil, enabling maximal growth and seed production of *R. crispus*.

The aim of this study was therefore to answer the following questions: (i) How are the number of leaves per plant, number of leaves per main stem, length of the longest leaf, plant height, number of stems per plant, seed production per plant, seed size and seed weight of *R. crispus* affected by nutrient availability? and (ii) How are the germination and chemical composition of seeds affected by the nutritional status of the mother plant?

Material and methods

Study site and design of the pot experiment

In May 2008, a pot experiment was established in the open-air vegetation-growing hall at the Crop Research Institute in Prague-Ruzyně (Czech Republic, 50°5′7.574″N, 14°18′13.286″E) with ambient rain, temperature and light conditions (Křišťálová *et al*., 2011). Ten fertiliser treatments were applied: Control, N_1, N_2, P_1, P_2, K_1, N_1P_1, $N_1P_1K_1$, $N_2P_1K_1$, $N_2P_2K_1$, (see Table 1 and Fig. 1 for details). Each treatment was replicated five times (thus 50 pots altogether). The pots were fertilised twice in 2008 and 2009 on 12 May and 20 July each year using the following fertilisers: ammonium nitrate with lime (NH_4NO_3 + $CaCO_3$, 27.5% N, 10% Ca), super phosphate [$Ca(H_2PO_4)_2$ + $CaSO_4$, 8.5% P, 20% Ca, 10% S] and potassium chloride (KCl, 50% K, 47% Cl).

Table 1 List of fertiliser treatments and amount of nutrients applied in one dressing (in kg of N, P and K per ha)

Treatment abbreviation	N (kg ha^{-1})	P (kg ha^{-1})	K (kg ha^{-1})
Controls	–	–	–
N1	150	–	–
N2	300	–	–
P1	–	40	–
P2	–	80	–
K	–	–	100
N1P1	150	40	–
N1P1K	150	40	100
N2P1K	300	40	100
N2P2K	300	80	100

Fig. 1 Photograph of selected fertiliser treatments taken on 14 June 2009. The size of individual *Rumex crispus* plants was greatly affected by fertiliser treatment. Treatment abbreviations are given in Table 1.

The position of individual pots was changed at weekly intervals to avoid any side effects. Pots were watered when necessary to avoid water stress.

The pot volume was 30 L, and the pot surface area was 1963 cm^2 (pot diameter, 50 cm, see Fig. 1). Clay soil with the following chemical properties was used: N_{total} = 919 mg kg^{-1}, $K_{MehlichIII}$ 160 mg kg^{-1} (good K availability), $P_{MehlichIII}$ 16 mg kg^{-1} (low P availability), $Mg_{MehlichIII}$ 373 mg kg^{-1} (high Mg availability), $Ca_{MehlichIII}$ 10 501 mg kg^{-1} (very high Ca availability) and pH/$CaCl_2$ of 7.96. Potassium-rich soil was used to avoid any risk of K limitation on growth, as the emphasis was on N and P nutrition in this study. To ensure that growth was not limited by K, treatments containing K (K, N_1P_1K and N_2P_2K) were included.

At the study site, the mean annual temperature was 8.2°C (ranging from 6.4 to 9.7°C), and the mean annual precipitation was 422 mm (ranging from 255 to 701 mm; Prague-Ruzyně meteorological station, 1955–2007). The mean temperature from June to September 2008 and 2009 (main vegetative season) was 17.6 and 17.9°C and from December 2008 and 2009 to March 2009 and 2010 (winter season), it was 2.4 and 0°C respectively. During the 2008/2009 winter season, the lowest measured temperature (−13.2°C) was recorded on 3 January 2009, and during the 2009/2010 winter season, the lowest temperature (−19.8°C) was recorded on 27 January 2010 (Meteorological station of the Crop Research Institute Prague-Ruzyně; http://www.vurv.cz/meteo). Pots were not protected by covering or insulated from frost and were exposed to normal weather conditions during the winter.

Seeds of *R. crispus* were collected during autumn 2007 from a region near Prague city in the central part of the Czech Republic. The collection sites were mainly roadside ditches or abandoned fields. Seed material was collected from a group of plants at three nearby localities. Five plants were randomly selected at each site, taking care not to favour tall or small plants. Twenty visually undamaged and fully ripened seeds of *R. crispus* were sown into each pot with pre-fertilised soil on 19 May 2008. All but three of the most well-developed plants were removed from each pot on 26 June 2008. The experiment was terminated in April 2010, as no plants survived the 2009/2010 winter season. Mechanical weeding took place throughout the experiment.

Data collection

The effect of nutrient availability on the emergence and early growth of *R. crispus* was studied by Křišťálová *et al.* (2011) in the first vegetative season in 2008. No flowering or formation of stems was recorded in the first vegetative season, and plants terminated the season as rosettes in all treatments. From the beginning of the second vegetative season in 2009, the following data were collected at 2-week intervals: (i) number of leaves per rosette, (ii) number of leaves per main stem, (iii) length of the longest leaf, (iv) height of the plant and (v) number of stems per plant. Fertile stems with fully ripe seeds were harvested 5 cm above ground level on 9 August 2009. All achenes were collected from each stem, dried at room temperature (22°C) and weighed along with the perianth. The weight of 1000 seeds without the perianth was also measured, and the proportion of the weight of the perianth (49% of weight of achenes) was determined, and seed production per individual plant calculated. The length and width of 200 seeds from each treatment were measured using a light microscope equipped with the image analysis software Analysis (Olympus, Tokyo, Japan (http://www.olympus-global.com).

The concentration of total nitrogen in seeds (without perianth) was determined via the Dumas method using the Dumatherm Nitrogen Determination System (http://www.gerhardt.de). Phosphorus and potassium concentrations were determined by spectrophotometry and emission flame spectrometry after digestion in sulphuric acid, in an accredited national laboratory. Only one mixed sample of seeds was analysed per treatment owing to insufficient production of seeds in several treatments.

Germination experiment

Following harvest on 9 August 2009 to the start of the germination experiment on 18 June 2010, seeds were stored in stable laboratory conditions (room temperature, 20°C) in paper bags in the dark. Seeds of many *Rumex* populations are dormant when persisting on dry stems (Martinková & Honěk, 2001). Therefore, a long after-ripening period under room conditions that elapsed between the harvest and the germination experiment was used to remove the dormancy. Only full and entire seeds collected from senescent and almost dry stems were used. The germination test was carried out in a klimabox using 90-mm-diameter Petri dishes containing KA2 filter paper regularly dampened with distilled water to avoid seed desiccation. Light conditions were set to a long-day photoperiod alternating 16 h light and 8 h dark under constant temperature (20°C). Three replicates of 50 seeds were used for each fertiliser treatment. Germination was observed daily for a period of 3 weeks.

Data analysis

All analyses were conducted using STATISTICA 8.0 software (Statsoft, Tulsa, Oklahoma). One-way and repeated measures ANOVA followed by comparison using Tukey's HSD test were conducted to identify significant differences between treatments, time and their interactions. The relationship between seed length and width was evaluated by linear regression analysis.

Results

Plant characteristics

In the first year of the study (2008), only rosettes developed in all treatments. All rosettes survived the 2008/2009 winter season and started to grow again in spring 2009. During the second vegetative season in 2009, the number of stems per plant, number of leaves per rosette, number of leaves per main stem, plant height and length of the longest leaf in the rosette were high in all treatments where N and P were applied together, but low in the control and treatments in which N, P and K were applied separately. The effects of treatment, time and the treatment by time interaction were significant on all measured plant characteristics (Table 2).

The size of rosettes was greatly affected by fertiliser treatment in spring 2009. On 11 April 2009, the mean number of newly arising stems ranged from < 1 in the control to almost five in the N1P1 treatment, and the number of leaves in the rosette ranged from 2 to 22 in the same treatments (Figs 2 and 3A). In almost all treatments, the number of newly arising stems decreased slightly between April and May and was then stable up to the mid-August harvest. Plant regrowth and the formation of new rosettes with growing points and leaves were recorded at the end of August. The number of leaves per rosette was highest on 24 May. Later on, the leaves of the rosettes disappeared as the expanding leaves on the stems shaded the rosettes, the leaves of which subsequently died. The number of leaves on the main stem was highest on 19 June and then decreased as the lower leaves died and disappeared (Fig. 3B). On 19 June, the number of leaves per main stem ranged from 2 in the control to 12 in the N1P1K and N2P1K treatments. Plant height rapidly increased between 9 May and 5 June, particularly in the N1P1, N1P1K and N2P1K treatments (Fig. 3C). The period from 9 May to 5 June was the main stem elongation period. On 3 July, plant height ranged from 21 cm in the control, P1 and P2 treatments up to 125 cm in the N1P1, N1P1K and N2P1K treatments. The longest leaves in rosettes were recorded in the period from 9 to 24 May. On 24 May, the length of the longest leaves ranged from 5 cm in the P1 treatment up to 43 cm in the N2P1K treatment. No plants survived the 2009/2010 winter season, and no living plants were recorded in April 2010.

Table 2 Results of repeated measures ANOVA of number of stems per plant, number of leaves per rosette, number of leaves per main stem, plant height and length of the longest leaf in the rosette

Tested variable		Treatment	Time	Treatment x time
No. of stems per plant	*F*	66	60	3.7
	P	< 0.001	< 0.001	< 0.001
No. of leaves per rosette	*F*	52	172	8.2
	P	< 0.001	< 0.001	< 0.001
No. of leaves per main stem	*F*	25	132	7.2
	P	< 0.001	< 0.001	< 0.001
Plant height	*F*	32	227	6.2
	P	< 0.001	< 0.001	< 0.001
Length of the longest leaf in the rosette	*F*	42	140	5.1
	P	< 0.001	< 0.001	< 0.001

Degrees of freedom: nine for treatment, 10 for time and 90 for treatment by time interaction.

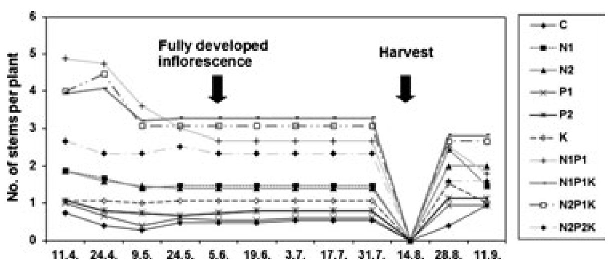

Fig. 2 Effect of fertiliser treatment on mean number of stems per plant. Treatment abbreviations are given in Table 1.

Seed production

The number of seeds per plant was greatly affected by fertiliser treatment and ranged from < 2000 in the control and P1 treatment up to almost 25 000 in the N2P2K treatment (Table 3). More than 16 000 seeds were produced per plant in all treatments in which N and P were applied together.

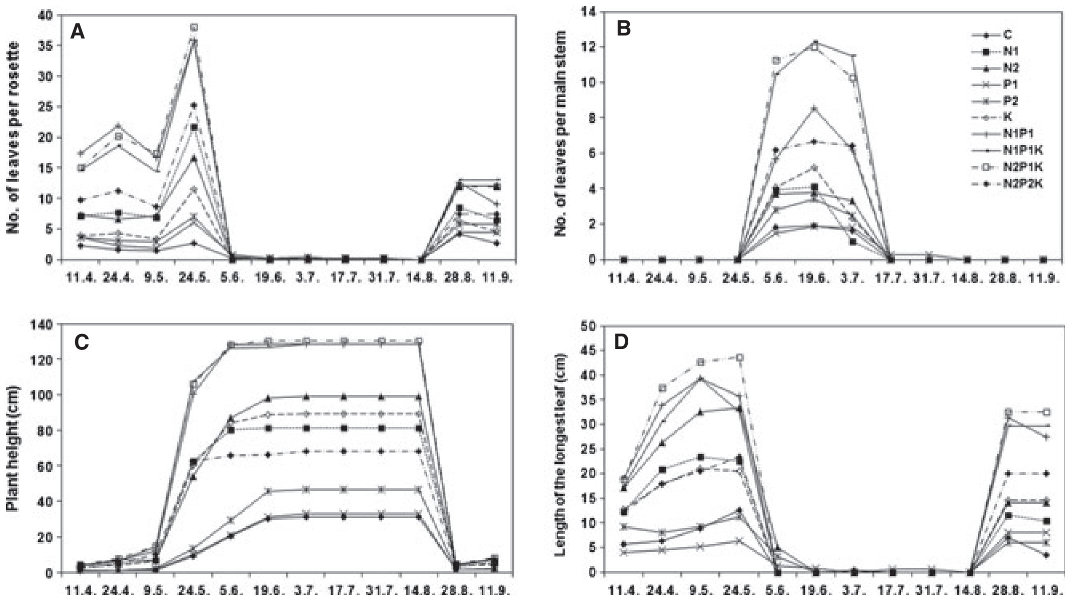

Fig. 3 Effect of fertiliser treatment on (A) number of leaves per rosette, (B) number of leaves per main stem, (C) plant height and (D) length of the longest leaf. Treatment abbreviations are given in Table 1.

Table 3 Mean seed production per individual plant and concentration of N, P and K (in g kg^{-1}) in seeds of *Rumex crispus* from different treatments. Treatment abbreviations are given in Table 1

Treatment abbreviation	Seeds per plant	N	P	K
Controls	1831	19.9	4.0	5.1
N1	11 443	20.7	3.0	2.9
N2	9512	22.0	2.7	2.5
P1	1575	20.9	4.1	5.3
P2	3080	21.2	4.0	5.3
K	2815	18.6	3.6	4.1
N1P1	17 617	19.7	3.7	4.4
N1P1K	16 750	19.7	3.8	4.2
N2P1K	20 982	21.6	3.1	3.2
N2P2K	24 932	21.6	3.5	3.7

Seed chemical composition, weight, length and width

The N concentration in seeds ranged from 18.6 g kg^{-1} in the K treatment up to 22.0 g kg^{-1} in the N2 treatment; the P concentration ranged from 2.7 g kg^{-1} in the N2 treatment up to 4.1 g kg^{-1} in the P1 treatment and the K concentration ranged from 2.5 to 5.3 g kg^{-1} in the P1 and P2 treatments respectively (Table 3). The weight of 1000 seeds was significantly affected by treatment and was <1.3 g in the N1, N2 and N1P1K treatments and above 1.5 g in the control, P2, N2P1K and N2P2K treatments (Fig. 4A). Seed length and width were significantly affected by treatment (Fig. 5A,B). Seeds shorter than 2.1 mm were recorded in the N2 and N1P1K treatments, while seeds longer than 2.2 mm were recorded in the control, P1, P2, N2P1K and N2P2K treatments. Seed widths lower than 1.45 mm were recorded in the N1, N2, K, N1P1 and N1P1K treatments, and seeds wider than 1.45 mm were recorded in the control, P1, P2, N2P1K and N2P2K treatments respectively. Seed length and width were significantly positively correlated (Fig. 5C).

Seed germination

Seed germination and the time required for the 50% of the seeds to germinate were significantly affected by treatment (Fig. 4B,C). With the exception of the N2 treatment (80% germination) and N1 and N1P1K treatments (95% germination), seed germination was above 95% in all treatments. One hundred per cent seed germination was recorded in the control, P2, K and N2P1K treatments.

With the exception of the N1 and N2 treatments, the time required for the germination of 50% of seeds was approximately 2.6 days. In the N1 and N2 treatments, it was 3.2 and 3.6 days respectively.

Discussion

Plant characteristics

Large differences in plant height and number of stems or leaves can be recorded even in plants of the same origin under different nutrient availability. The phenotypic plasticity of *R. crispus* is high, and plant characteristics such as plant height, number of stems, and number and size of leaves must be interpreted with caution when

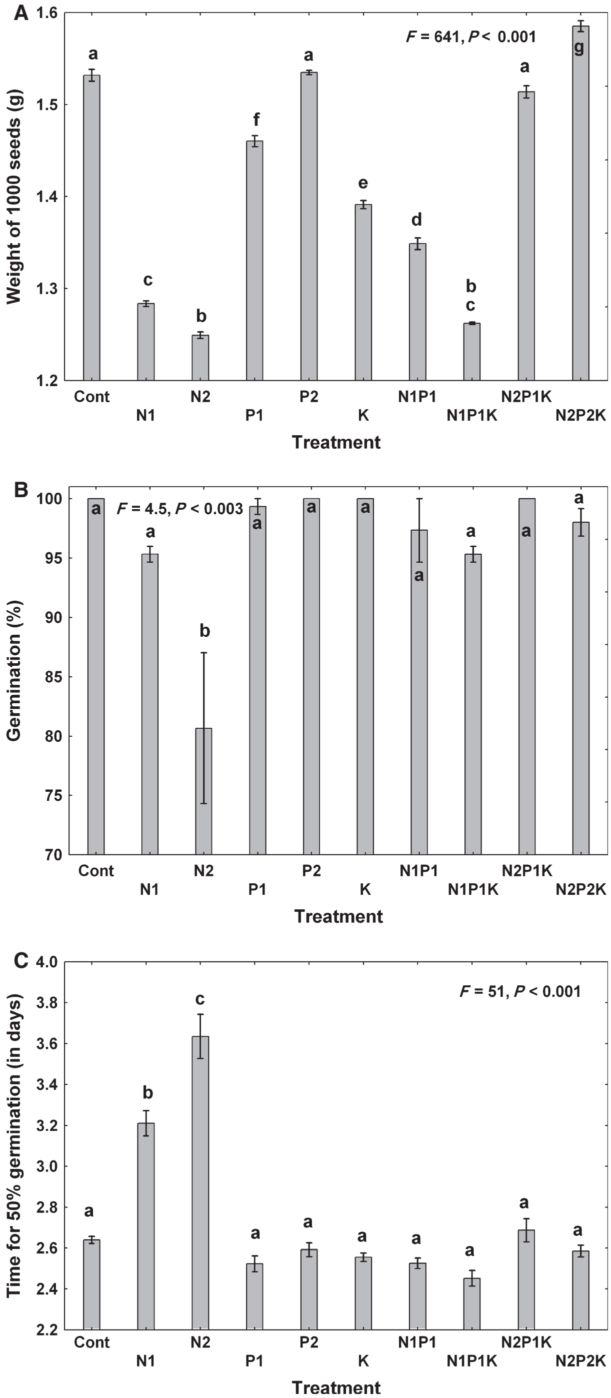

Fig. 4 (A) Weight of 1000 seeds without perianth, (B) germination and (C) time required to achieve 50% germination. Seeds of *Rumex crispus* were collected from individuals planted in different fertiliser treatments. Treatment abbreviations are given in Table 1. Vertical lines represent standard error of the mean (SE), and *F* and *P* values were obtained from one-way ANOVA. According to the Tukey's test, treatments with the same letter were not significantly different.

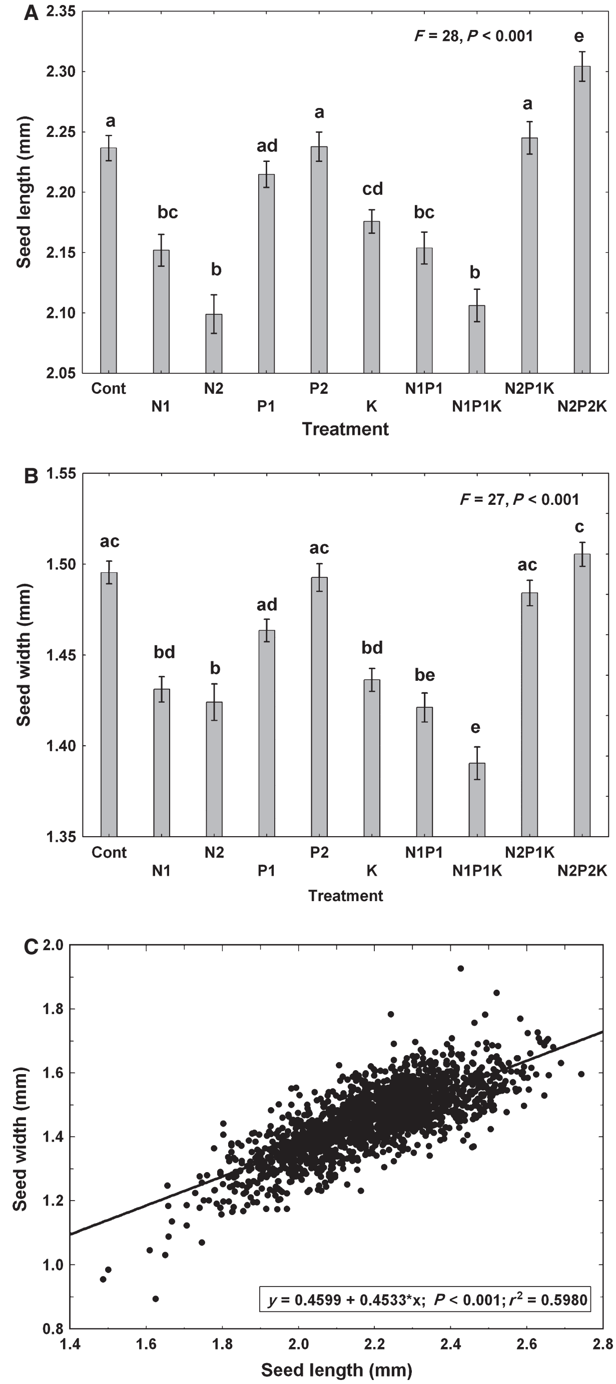

Fig. 5 Effect of fertiliser treatment on (A) seed length (B) seed width and (C) correlation between length and width. Treatment abbreviations are given in Table 1. Vertical lines represent standard error of the mean (SE), and *F* and *P* values were obtained from one-way ANOVA. According to Tukey's test, treatments with the same letter were not significantly different.

describing different populations, as quantitative characteristics can be markedly affected by nutrient availability. For example, the maximum plant height of *R. crispus* (130 cm) recorded in this study was lower than the maximum height (150 cm) given in the flora of Germany (Rothmahler *et al.*, 2000), but higher than the maximum height (100 cm) given in the flora of the Czech Republic (Hejný & Slavík, 1990). It seems that the maximum height of *R. crispus* plants under optimum N, P and K nutrition and water availability and in the absence of competition from other species is 130 cm.

In our study, *R. crispus* behaved strictly as a biennial monocarpic species, although Grime *et al.* (1988) described *R. crispus* as a short-lived polycarpic perennial. Rosettes developed in the first vegetative season and stems, flowers and fruits in the second season. Although regrowth of plants and the formation of new rosettes were recorded after harvesting dry stems with fully ripe achenes in mid-August 2009, no plants survived the 2009/2010 winter season. We cultivated *R. crispus* plants of the same origin in field conditions under a two-cut management regime, performed in May and August. Cutting before or during flowering enabled some plants to survive for 4 years in permanent grassland (Strnad, 2011). The positive effect of cutting on the survival of *R. crispus* was also reported by Hongo (1989). Therefore, it seems that *R. crispus* can behave as a perennial if cut early, but not if cutting takes place at the ripe seed stage. It is highly likely that at least some populations of *R. crispus* in central Europe are monocarpic, rather than polycarpic.

Seed production

Seed production by *R. crispus* varies, depending on nutrient supply. In comparison with the nutrient-poor control, seed production was increased 14-fold by optimal N, P and K availability. Such a high increase in seed production was attributed to (i) an increase in the number of fertile stems per plant (Fig. 2) and (ii) an increase in the number of seeds per individual stem. The highest number of seeds produced under optimal nutrient and water supply was 24 932 seeds per plant. This was substantially lower than the values of over 40 000 seeds per plant mentioned in a review by Cavers and Harper (1964) and frequently referred by other authors (Zaller, 2004; Bond *et al.*, 2007). It seems that 40 000 seeds per plant may have been an overestimate. For example, Hume and Cavers (1983b) recorded seed production per individual plant of 28 300 seeds under optimal growth conditions in the garden, Stevens (1932) recorded 29 500 under the same growth conditions, and Bentley *et al.* (1980) only 3900 seeds per plant under normal pasture management. Based on our results and their comparison with the results of the other authors, we estimated the maximum seed production per individual plant of *R. crispus* to be 30 000.

Seed chemical composition, weight, length and width

Nutrient availability in the soil and therefore the nutritional status of the mother plant greatly affect the concentrations of N, P and K in the seeds of *R. crispus*. For example, the concentration of N in seeds was above 2.15% only in treatments with a high N supply (N2). This positive effect of N application on N concentration in seeds is well known from grain crops (Acreche & Slafer, 2009), but has not been reported for *R. crispus* previously. Similarly, P and K concentrations were positively affected by P and K application. The lowest P and K concentrations in seeds were recorded in the N1 and N2 treatments, probably due to the restricted P and K supply and the dilution effect caused by the increased growth of plants owing to the improved N supply. The weight of 1000 seeds, ranging from 1.25 in the N2 to 1.58 g in the N2P2K treatment, was comparable with data published by other authors. According to Cavers and Harper (1964), the normal weight of 1000 seeds ranges from 1 to 2 g; Bentley *et al.* (1980) reported a range of 1.45 to 1.9 g and Hume and Cavers (1983b) a range of 1.25 to 1.72 g. The most interesting result was the high weight of individual seeds in the control, along with the low number of seeds and low weight of seeds in the N1 and N2 treatments, in which low P and K concentrations in the seeds were caused by an insufficient P and K supply. The length and width of seeds were highly positively correlated and reflected the weight of seeds in particular treatments. A high nutrient supply can therefore increase the number of seeds produced per individual plant, but need not increase the weight of individual seeds.

Seed germination

Seed germination may be affected by the nutritional status of the mother plant and therefore by nutrient concentrations in the seeds. Although the germination of *R. crispus* has been investigated previously (Cavers & Harper, 1966; Baskin & Baskin, 1985; Honěk & Martinková, 2001; Pye & Andersson, 2009), no study has investigated the effect of the nutritional status of the mother plant on the germination of its seeds. It seems that P and K concentrations of below 0.3% in seeds negatively affect their total germination and rate of germination and this is in accordance with the results given by Hrdličková *et al.* (2011) for *R. obtusifolius*. Further, this was demonstrated by the lowest rate of germination of seeds from the N2 treatment, which had the lowest P and K concentrations and seed size. Lower rates of germination of small compared to large seeds of *R. crispus* were recorded by Cidecyian and Malloch (1982), but no information was provided about the chemical composition of the seeds. A maternal nutrient effect on the germination of seeds and the performance of offspring was also recorded for several other species, but its connection with the chemical composition of the seeds has rarely been investigated (Miao *et al.*, 1991;

Wulff *et al*., 1999; Latzel *et al*., 2009). Some of the viability in seed germination can therefore be determined by the concentration of P and K in the seeds, which in turn is dependent on the nutritional status of the mother plant.

Conclusions

A typical feature of *Rumex crispus* is high phenotypic plasticity in plant height, number of leaves, length of leaves, number of stems and seed production per plant in relation to N, P and K availability in the soil. To produce a large quantity of rapidly germinating seeds, *R. crispus* requires a balanced N, P and K supply. Deficiency of P and K supply to the mother plants, together with a high N supply, can result in the production of P- and K-deficient seeds (P and K < 3 g kg^{-1}) with a lower capacity for germination. In central Europe, at least some populations of *R. crispus* do not flower in the seeding year and are strictly monocarpic. Given the short lifespan and monocarpic character of the species, control is probably most effective at the rosette stage, prior to the production of viable seeds. Without seed production and regeneration through seedlings, *R. crispus* will find it difficult to establish long-term viable populations.

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