



Original article

Life-history variation in the short-lived herb *Rorippa palustris*: The role of carbon storageMonika Sosnová^{a,b,*}, Jitka Klimešová^b^a Department of Botany, University of South Bohemia, Branišovská 31, CZ-370 05, Czech Republic^b Institute of Botany, Academy of Sciences of the Czech Republic, Dukelská 135, CZ-379 82 Třeboň, Czech Republic

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ABSTRACT

Carbon storage is commonly found among perennials, but only rarely in annuals. However, many short-lived species may behave as annuals or short-lived perennials depending on the date of germination, photoperiod or disturbance. Due to the trade-off between investments into current reproduction vs. survival, these life-history modes presumably differ in carbon allocation. In this study, we aimed to evaluate how carbon storage is affected by germination date and disturbance in an outdoor pot experiment with the short-lived *Rorippa palustris*. Plants from autumnal and summer cohorts were injured in different ontogenetic stages (vegetative, flowering and fruiting) and the starch content in roots was assessed. Plants from the autumnal cohort invested more carbon into growth and reproduction, whereas plants from the summer cohort invested preferentially into reserves. However, injury changed the allocation pattern: in plants from the autumnal cohort, injury prevented allocation to reproduction and thus injured plants had a larger carbon storage at the end of the season than control plants; injury at the flowering and fruiting stage caused depletion of reserves for regrowth in plants from the summer cohort, resulting in lower starch reserves compared to control plants. We suggest that life-history variation in *R. palustris* can be caused by changes in its carbon economy: when all resources could not be used for flowering due to weak photoinduction or loss of flowering organs due to injury, part of the resources is stored for over wintering and reproduction in the next year.

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1. Introduction

Carbon, which is the main building component of the plant body, can be allocated to growth, defense, storage or reproduction (Chapin et al., 1990). However, different patterns of carbon investments result in different life-history strategies (Stearns, 1992). Carbon is stored at the time of its surplus for later use for reproduction, survival in changing conditions or regrowth following disturbance or herbivory (Iwasa and Kubo, 1997; Suzuki and Steufer, 1999). The amount of stored resources changes over time and with plant ontogeny. In perennials, the lowest amount of stored carbon is found at the time of intensive growth (Mooney and Billings, 1960; Steinlein et al., 1993; Wyka, 1999), before flowering (Chapin et al., 1990) and at the time of seed ripening (White, 1973). In temperate conditions, starch concentration increases before the end of the growing season and attains its maximum before over

wintering (Steen and Larsson, 1986; Suzuki and Hutchings, 1997). On the contrary, annuals invest carbon preferentially in fast growth and an early start of reproduction rather than in storage. In the desert winter annual *Plantago insularis* var. *fastigiata* and in the wetland annual *Senecio aquaticus*, the highest carbohydrate levels were found in young vegetative plants and were exhausted during seed ripening (Dina and Klikoff, 1974; Otzen, 1977). Thus, annual plants are generally “income breeders” (sensu Jönsson, 1997), even if they store some carbon before the start of reproduction. Larger storage was found in short-lived monocarps with longer life-span (Clark and Burk, 1980; Chiariello and Roughgarden, 1984; Vilela et al., 2008).

The intermediate life-history strategy between annual and polycarpic perennial is reported in short-lived perennials, where carbon storage is not wholly exhausted for reproduction. For example, carbon reserves found before the onset of winter in the short-lived perennial *Senecio jacobaea* were higher compared to the annual *S. aquaticus*, but lower than in the perennial *Senecio erucifolius* (Otzen, 1977). Carbohydrate reserves in this species declined significantly during the generative stage, but still remained at a relatively high level enabling further vegetative reproduction (Otzen, 1977). Some plant species may exhibit life-history variation

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due to interactions with germination cueing, size- or vernalization-dependent flower induction or injury (Klinkhamer et al., 1987; Klimešová et al., 2007). The resulting ability to function either as an annual, biennial or short-lived polycarpic perennial might be crucial for survival in environments with unpredictable disturbance events. This plasticity also provides a useful model for studying allocation trade-offs between investment into recent and future reproduction, and/or survival.

In this study, we aimed to evaluate the pattern of allocation of storage assimilates during the life cycle of *Rorippa palustris* with respect to life-history variation. *R. palustris* is a short-lived species with the ability to change its life-history mode according to the date of germination, injury to the plant body and photoperiod, which is responsible for inducing reproduction (Klimešová et al., 2007). Plants germinated in April or Jul./Aug. were observed to have an annual mode, whereas plants germinated during the summer months (around the summer solstice) showed a polycarpic perennial mode (Klimešová et al., 2007). This is caused by the ability of seeds to germinate throughout the whole season (Grime et al., 1988) together with photoperiodically induced flowering, which occurs in long day conditions, i.e. plants germinating before the summer solstice flowered in the same season (summer annuals), whereas plants germinating afterwards postponed flowering to the next season (winter annuals). Moreover, plants germinating round summer solstice were able to reproduce twice, i.e. in the first and second year of their life (polycarpic perennials) (Klimešová et al., 2007).

Life-history mode in *R. palustris* can also be altered by severe injury, when all aboveground biomass is removed and the plant is forced to resprout from the roots. New sprouts emerging after a severe injury are not initialized for flowering, if the disturbance occurs after the summer solstice. This resulted in the postponement of reproduction to the next season (Klimešová et al., 2007).

These variable life-history modes should be reflected in carbon storage which presumably increases in time of undisturbed vegetative growth and decreases after injury or due to flowering. Moreover, shortening day-length will trigger carbon allocation preferentially to storage rather than growth, as we observed in the study with several cohorts of *R. palustris* grown under different photoperiods. Plants growing in short day – autumnal – conditions invested more in belowground biomass compared to plants growing in long day – spring – conditions (Martínková et al., 2004). Thus, we expect that all these intrinsic and extrinsic factors will conjointly affect the resulting autumnal budget – a prerequisite for over wintering and repeated reproduction.

2. Materials and methods

2.1. Pot experiment

A common garden experiment with plants of *R. palustris* was carried out from August 2003 to November 2004. Two cohorts, each containing 160 plants, were planted in August 2003 (autumnal cohort) and June 2004 (summer cohort) and represented winter annual and short-lived perennial life-history modes, respectively (Klimešová et al., 2007).

Seeds of *R. palustris* from an outdoor cultivation in Třeboň and collected in 2002 were germinated on moist filter paper in Petri dishes under fluctuating temperatures approximating 25/5 °C day/night. Seven days after germination, seedlings were planted into pots (one seedling per pot, 14 × 14 × 16 cm) filled with a mixture of pure washed sand and standard garden soil (AGRO CS a. s., Česká Skalice) at a volume ratio of 1:5. A fine-textured textile was placed on the bottom of each pot to avoid root penetration. Pots were placed into containers (200 × 120 × 40 cm, 80 pots/container)

located in a common garden and watered regularly to be moist, but not waterlogged or dry. Plants were fertilized every 5 weeks during the growing season with a tablet fertilizer (Universal garden fertilizer, ASB Grönland, nutrient content: N 0.1g/pot, P 0.06 g/pot, K 0.7 g/pot); the first tablet was added immediately after planting. Plants planted in August 2003 overwintered outdoors without frost protection nor with any water and nutrient additions.

2.2. Injury

During the vegetation 2004 season, randomly chosen plants from both cohorts and containers were injured in three ontogenetic stages: vegetative rosette (40 replicates for each cohort), flowering plants (40) and fruiting plants (40). All aboveground biomass, together with the root crown, was removed at the time of injury, i.e. all axillary buds were removed, therefore only regeneration from adventitious buds on roots was possible (Klimešová et al., 2007). For implementation of the injury, the appearance of the plant rather than age was important. The timetable of the experiment is shown in Table 1. Regeneration of plants, rosette diameter, height and number of flowering shoots were followed. Experimental injury aimed at imitating severe disturbances occurring due to human activity on ruderal places or water erosion in natural populations.

Control plants were divided into four groups, 10 plants were left intact while the others were harvested in three ontogenetic stages, i.e. vegetative, flowering and fruiting plants (10 plants for each stage). The biomass was separated into aboveground and belowground structures, oven dried (80 °C/24 h) and weighed. Belowground biomass was used for determining starch concentration in roots for a given ontogenetic stage.

The experiment was terminated in the beginning of November 2004, when plants started to shed leaves and all seeds were ripe and fell out. Regenerated plants from both cohorts together with intact control plants were carefully removed from pots and separated into above/below-ground biomass. The aboveground biomass consisting of dry shoots and, in regenerated plants, small vegetative rosettes of new leaves, was dried (80 °C/24 h) and weighed. The belowground (root) biomass was dried (80 °C/24 h), grinded with laboratory vibratory mill (Pulverisette 9, fa. Fritsch) and used for assessment of the starch content.

2.3. Starch analysis

Starch content in roots of control plants harvested in different ontogenetic stages and injured plants at the end of the vegetation season was determined using the amyloglukosidase/ α -amylase method (McCleary et al., 1997). In the first step, the starch was partially hydrolyzed and totally soluted while in the second step the starch dextrans were quantitatively hydrolyzed by amyloglukosidase (method AA/AMG 11/01, Total starch assay procedure, kit by Megazyme). Glucose, the product of the hydrolysis, was then colored using GOPOD (Glucose determination reagent) and its content was assayed spectrophotometrically (510 nm, Spekol 210).

2.4. Statistical analysis

The effects of cohort and ontogenetic stage in control and regenerated plants were tested by split-plot design analysis of variance (linear mixed-effects model), with container as a random factor. This analysis enables comparison of not completely randomized design with plants placed in 2 × 2 containers (split-plots).

Difference between control intact plants and regenerated plants from a respective ontogenetic stage (vegetative, flowering and fruiting plants) in all measured parameters was tested by

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