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Water limitation effect on seed development and germination in *Trigonella coerulea* (Fabaceae)

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Abstract

The annual garden spice legume *Trigonella coerulea* was subjected to controlled drought conditions to investigate the influence of resource limitation on flowering, seed production and germination. Limitations in water availability significantly reduced plant height and the number of fruits produced. However, treatments had no significant effect on seed set within the fruit. Fruit number per plant, rather than seed number per fruit was affected by resource limitation. Plants growing under water deficiency had higher flower abortion rates. Simultaneously, the size and germination rate of the seeds were decreased. In terms of reproductive success *T. coerulea* was not able to adapt reproduction to water shortage. Increase in moisture had no significant effect on seed quantity and quality when compared to the control.

Keywords: Drought; Reproductive success; Seed development; Germination; Seed set

Introduction

Trigonella coerulea (L.) Ser. is a garden spice legume widely cultivated in Georgia. The powder of grained seeds of this plant is used as spice almost in all traditional Georgian dishes. It was interesting to test whether water availability will affect seed productivity and quality in this plant species. Further, *T. coerulea* presents an interesting opportunity to study effects of resource limitation on seed set characters. In this plant species, normally four ovules are initially formed within the ovary and usually only two of them develop into mature seeds. However, there are pods containing one or three mature seeds and very rarely all four ovules within an ovary produce mature seeds. Consequently, even if double seededness might be considered as the typical pattern of seed set for *T. coerulea*, there is no fixed rate of ovule abortion and fluctuations in the number of seeds per fruit occur. Therefore, it seems to be of interest to investigate whether the number of seeds matured per fruit in this plant species will vary depending on resource limitation.

The abortion of potentially viable immature seeds and fruits between anthesis and dispersal has gained increased attention from plant ecologists during the last two decades (Stephenson, 1981; Wiens, 1984). The general questions to answer are, first, why plants produce many more flowers than fruits and, second, which fruits and seeds should a plant abort to maximise maternal reproductive effort. Current theories concerning the possible causes and function of flower and seed abortion provide two types of answers. One group of

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hypotheses focuses on environmental factors as causal of seed abortion, i.e. pollen availability (Agren, 1996; Trueman and Wallace, 1999), limiting of resources acquired for fruit and seed development (Lee and Bazzaz, 1982), influence of predators (Krupnick and Weis, 1999), pathogens (Jones, 1976) or unfavourable abiotic factors (Lee and Bazzaz, 1982), and effects of spatial structure and size of populations (Morgan, 1999; Nishihiro and Washitani, 1998). A second group of hypotheses is that the female reproductive effort in plants may not result from ambient environmental conditions or lack of fertilisation but is mainly genetically controlled (Casper and Wiens, 1981). This assumption has been supported by several studies, which show that the probability of the offspring survival is determined by intrinsic factors. E.g. competition among gametophytes or embryos of different genetic quality (Härdling and Nilsson, 1999; Lee, 1984; Queller, 1983), pistillate sorting (Gibbs and Sassaki, 1998), interactions between endosperm and embryo (Carputo et al., 1999), lethal mutations of female gametophytes (Christensen et al., 1998), or direct control from the parent plant (Charnov, 1979; Grossniklaus et al., 1998). The selective abortion hypothesis is an important factor explaining the advantage of the "surplus production" of ovules (Melser and Klinkhamer, 2001).

Casper and Wiens (1981) and Wiens et al. (1987) found that resource limitation has no overall effect on seed set characteristics in plant species with a constant number of seeds per fruit. This phenomenon, when the number of initially formed ovules within an ovary is reduced during seed formation by abortion to the constant number of seeds matured per fruit, is called a fixed rate of ovule abortion (Casper and Wiens, 1981). It occurs regardless of pollen availability or fluctuating environmental conditions. In other plant species, however, a clear correlation between seed set and limitation of resources and pollen availability has been demonstrated (Genter et al., 1997; Stephenson, 1984; Trueman and Wallace, 1999). It should be mentioned, that there is no fixed rate of seed abortion in most plant species, where resource limitation leads to the diminishing in seed number per fruit. In these plants the fluctuation in seed number correlates with the available resources. Against this background the annual legume *T. coerulea* with no fixed rate of ovule abortion represents an interesting opportunity to study effect of resource limitation on seed set characters.

In the present study, we subjected *T. coerulea* plants to limitations in water availability to investigate how resource limitation influences seed development and germination. The questions addressed were: (1) Does limitation in water availability alter the proportion of resources allocated to reproduction, i.e. the numbers of flowers, fruits, ovules and seeds produced, and reproductive phenology? (2) Do percentages of fruit and seed abortions vary in relation to environmental conditions? (3) Does resource limitation influence seed filling patterns and seed mass? (4) Does the germination ability of seeds differ depending on the environmental conditions during seed development?

Materials and methods

Trigonella coerulea (L.) Ser. (= *T. caerulea* (L.) Ser.) is an annual spice legume cultivated in gardens (Lachashvili, 1981). Stems are erect with 20–100 cm height. Inflorescences are globose heads, consisting of many pealike, blue, bisexual flowers. There are four ovules initially formed within an ovary. The plant is an obligate outcrosser. Pods are obovate-rhomboid, 3–4 mm long. They usually contain two mature seeds, however, some may possess one, three or rarely four seeds. The seeds are ca. 2 mm long, and seed coat colour is yellow, brown or black indicating large genetic variation.

For this experiment the following selection steps were chosen to reduce the genetic variability. Seeds of *T. coerulea* were collected on one site from plants cultivated under standard conditions in Georgia. The seeds were sorted according to size and seed coat colour. Seeds with a black coloured pigmentation of the seed coat and a length of 2–2.5 mm were used for the present experiment, because, they showed highest germination percentages (Akhalkatsi and Lösch, 2002). The seeds were kept in paper bags at room temperature.

Seeds were sown in three plots differing in moisture conditions. (1) *Control* – plants were growing in full sun (photosynthetic photon flux density (PPFD) averaged $1800 \pm 400\,\mu mol\,m^{-2}\,s^{-1}$) and were watered once in 1–2 days so that the soil moisture was maintained near field capacity, $57.4 \pm 8.3\%$. (2) *Drought* treatment was conducted according to Pyke (1989). The plants were subjected to drought stress from day 21 after germination on throughout the experiment (90 days). The soil was allowed to dry for 4–5 days and was watered only after the target plant leaves had been wilting for 48 h. Afterwards, the plot was saturated with water and the drought procedure was repeated until the fruits had matured at which time they were harvested. Mean soil moisture before rewatering was $42.3 \pm 6.7\%$. (3) *Moist condition* – plants were grown in full sun, soil was saturated with water two times a day. Mean soil moisture was $75.8 \pm 3.6\%$.

The following characters were determined for each group of plants: plant height, duration of phenological phases, number of flowers and fruits per plant, number of ovules and seeds per fruit, fruit:flower ratio, seed:ovule ratio, relative reproductive success (RRS, defined according to Wiens (1984) as (fruit:flower ratio) × (seed:ovule ratio) × 100%), number of pollen