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Mapping a floral trait in Shepherds purse – 'Stamenoid petals' in natural populations of *Capsella bursa-pastoris* (L.) Medik

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ABSTRACT

Striking feature of angiosperm diversity is the huge number of variations in corolla morphology including complex innovations like variations in symmetry or the identity and number of floral organs. Throughout the Brassicaceae, the disymmetric flower structure is highly conserved. Still, quite a few floral alterations occur like a variant of Common Shepherds purse (*Capsella bursa-pastoris*), in which all petals have been transformed into additional stamens. This "decandric" phenotype has been reported for the first time about 200 years ago. In some of the original locations the variant has been recovered recently. The long term persistence indicates the establishment of an evolutionary novelty in wild populations in sympatric occurrence with wild-type plants. Due to this fact the floral variant has become an interesting model for evolutionary studies. The phenotype is heritable and just a single locus, termed "*Stamenoid petals*" (*Spe*), is assumed to be involved in the molecular origin. To unravel the chromosomal localization of this locus, a linkage map analysis was carried out using molecular markers (AFLPs, RAPDs). The final map includes 15 linkage groups and the floral trait was integrated on linkage group 12 (CBP12) including six AFLP markers. Out of these, five markers were successfully sequenced and revealed sequence identities with chromosome IV of the *A. thaliana* genome. Interestingly, *AGAMOUS* is located on this chromosome, the only class C floral organ identity gene in the *A. thaliana* genome, which is compatible with the assumption that *Spe* is an allele of *AGAMOUS* rather than a regulator of that gene.

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Introduction

Studies about natural variation in flower morphology have a long-standing tradition for botanical research and the vast number of floral variation is an outstanding characteristic for angiosperm diversity. Very prominent examples are doubled-flowered taxa, which have fascinated botanists for many centuries or even millennia (Meyerowitz et al., 1989). In some families, however, variation in flower morphology is rare and often restricted to single taxa. For instance, Brassicaceae (338 genera; ~3 .700 species) are characterized by a highly conserved floral *bauplan*. Alterations from the conserved 'brassicaceous' flower have been reported in only 5% out of all genera (Endress, 1992). Such modifications include the transition from disymmetrical to monosymmetrical flowers (e.g. *Iberis*, *Teesdalia*) or lack of petals (e.g. *Rorippa*, *Lepidium*, *Cardamine*, *Capsella*). An increased number of carpels and the occurrence of unisexual flowers are exceptional traits in just a few species (Appel and Al-Shehbaz, 2003; Endress, 1992). Reduction in the number of fertile stamens is very common within the genus *Lepidium* and also reported for *Hornungia*, whereas an increase in stamens has only been reported for one species (*Megacarpea polyandra* Benth., 24 stamens; Al-Shehbaz, 1986). Apart from this polyandric species another case of increase in the number of stamens has been reported for *Capsella bursa-pastoris* (L.) Medik.

In this naturally occurring floral variant of Sheperd's Purse all petals have been transformed into additional stamens through homeosis (Fig. 1). Since petals are replaced and not totally lost, the overall number of floral organs remains unaffected. About 200 years ago, the variant has been described for the first time by Opiz (1821), who gave a very detailed description of the morphology. Due to its ten stamens, the author named this phenotype 'decandric' and considered the variant as a new species, *Capsella apetala* Opiz. At about the same time, the variant has been also described for Vienna (Trattinnick, 1821) and surroundings of Frankfurt/Main (Becker, 1828). Additional reports came from Braunschweig (Wiegmann, 1823) and it was also mentioned in the *Flora Berolinensis* (Schlechtendal, 1823) and in the *Flora von Westfalen* (Beckhaus, 1893). Almquist (1923) described twelve variants of *Capsella bursa-pastoris* from northern Europe (mainly Sweden) showing apetalous flowers, but only one was characterized by ten stamens (*C. bursa-pastoris* (L.) *litoralis* f. *coronopus* E. AT). Murbeck (1918)

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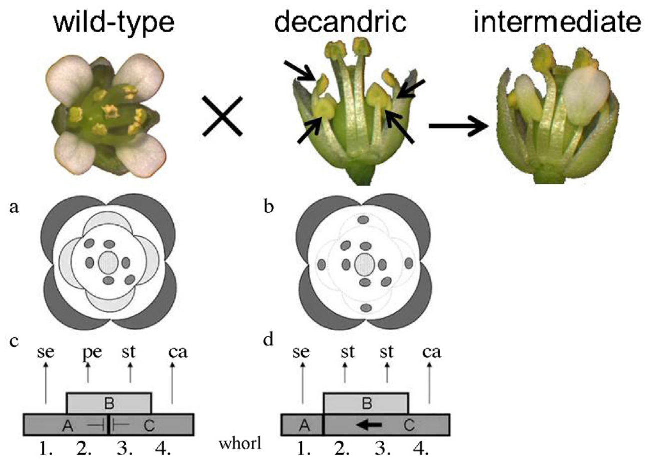

Fig. 1. Illustration of floral components in (a) wild-type and (b) decandric flowers of *Capsella bursa-pastoris*. Floral organs are arranged in four concentric whorls: The outer whorl is formed by sepals (se), followed by the petal whorl (pe). In the inner two whorls stamens (st) and carpels (ca) are established. The outlined formation of wild-type flowers is in accordance with the initial ABC model (c) whereas in the homeotic variant (d) the C function is ectopically shifted into the second floral whorl leading to additional stamens.

reported additional locations with decandric individuals of Shepherd's Purse in Berlin (Germany), Sweden (Sköfde, Norrköping) and another one from North America (South Dakota, Deadwood). Today, still a few populations are known from vineyards and ruderal hillsides in Germany (Nutt et al., 2006; Reichert, 1998), ruderal sites in Vienna (Austria) and in the Czech Republic from Brno and Prague (Hameister, 2013). In vineyard populations tens of thousands of individuals of this type occur while in the other stands only more or less single individuals can be found. In all these habitats, both floral variants (the one with petals – in the following named "wild-type" – as well as the "decandric" variant) occur sympatrically and decandric plants comprise about 10% of the populations. Reports from its occurrence around Prague, Vienna and Frankfurt/Main in the early 19th century and the recent discovery there suggest that the variant exists in these locations at least since decades (southwest Germany) or maybe even centuries (Vienna and Prague). This long time co-existence of wild-type and the variant in natural populations is a very rare case and as a matter of fact, makes the variant an interesting model for evolutionary studies.

Although the occurrence of 'false polyandry' in *C. bursa-pastoris* is probably the only example in the mustard family, this phenomenon is quite common in general. In his essay about '*Staminale Pseudapetalie*', Murbeck (1918) describes this kind of variation for numerous genera, especially in the Rosaceae (*Neviusia*, *Coleogyne*, *Cercocarpus*) and Papaveraceae (*Macleaya*, *Bocconia*). Within the genus *Capsella*, the occurrence of '*Staminale Pseudapetalie*' might be the consequence of an evolutionary series: breakdown of self-incompatibility, the reduction or total loss of petals and polyploidisation are common trends within the Brassicaceae and represent evolutionary tendencies which might be involved in speciation processes (Hurka et al., 2005). This underlines the supposed evolutionary significance of the decandric variant, and recently it has been chosen as a model system to study the ecological and molecular background of this floral variation (Hintz et al., 2006; Nutt et al., 2006). Yet, life-history traits were characterized (Ziermann et al., 2009; Hameister et al., unpublished) and the genetic differentiation among floral types in one vineyard population has been analyzed (Hameister et al., 2009). In the latter study, genetic differentiation into wild-type and decandric clusters could be detected which may indicate a recent divergence process. Additionally, ecotypic variation has been discovered, since the onset of flowering is significantly delayed in the decandric variant (Hameister et al., 2009). This divergence within a sympatric population together with the observation that fitness is not reduced in decandric plants, might characterize a recent speciation event (Ziermann et al., 2009). However, the most important requirement for any evolutionary meaning is the heritability of the novel trait. For the decandric *C. bursa-pastoris*, this has already been mentioned in its early reports (Opiz, 1821; Schlechtendahl, 1823; Dahlgren, 1919). Dahlgren's crossing experiments of wild-types with decandric *C. bursa-pastoris* revealed an approximately 1:2:1 segregation of plants with stamenoid, intermediate and petal organs in the second floral whorl. Recent segregation patterns of a cross between wild-type and decandric *C. bursa-pastoris* confirmed these reports and suggest a co-dominant inheritance of the phenotype (Nutt et al., 2006). The assumed single locus leading to the decandric phenotype has been termed *Stamenoid petals* (*Spe*) by Nutt et al. (2006). Taking account for the recent progress in molecular analyses of genetic principles that control precise establishment of floral organ identity, the decandric phenotype might be explained with the help of the ABC model. This model has been postulated in the early 1990s (Coen and Meyerowitz, 1991) based on studies of artificially induced floral mutants of *Arabidopsis thaliana* (L.) Heynh. and *Antirrhinum majus* L. The model states, that the identity of floral organs is specified by the activity of three classes of genes A, B, and C (for review, e.g. Krizek and Fletcher, 2005). This model was stepwise extended to a function D (Colombo et al., 1995) and a function E (Pelaz et al., 2000). Genes were identified for each class, which are involved in the genetic control of floral organ formation. The model indicates that only a few genes are required for accurate development of floral organs. In *A. thaliana*, for instance, there are two class A genes *APETALA1* and *APETALA2* (*AP1* and *AP2*), two class B genes, *AP3* and *PISTILLATA* (*PI*) and *AGAMOUS* (*AG*) as the class C gene. Applying the ABC model to the decandric *C. bursa-pastoris*, the transformation of petals into stamens might be the consequence of abnormal (ectopic) expression of a class C gene in the second (petal) whorl that may suppress the expression of class A genes (Fig. 1c and d; Hintz et al., 2006; Nutt et al., 2006). Indeed, phenotypes with stamenoid petals are known in artificial *A. thaliana* variants, involving ectopic expression of the class C gene *AGAMOUS* (Jack et al., 1997; Mizukami and Ma, 1992) or closely related *AG*-clade genes (Pinyopich et al., 2003). *AGAMOUS* or any other member of the *AG*-clade might be affected and therefore are the most valuable candidate genes to elucidate the corresponding phenotype with stamenoid petals in the second floral whorl.

The primary aim of the present study was the chromosomal localization of the putative *Spe* locus in a co-segregation analysis using a mapping population. The generated linkage map is based on molecular markers (AFLPs; Amplified fragment length polymorphisms), applying the advantage of reproducibility, genome-wide spread and high density of informative characters. Additionally, Random Amplified Polymorphic DNA (RAPD) markers were included to prove consistency with existing *C. bursa-pastoris* linkage maps (Linde et al., 2001). To constrain assumed candidate genes, a cross linkage to the genome of *A. thaliana* was carried out. The close relationship to *A. thaliana* may facilitate the studies, particularly because of high genome co-linearity (Acarkan et al., 2000; Boivin et al., 2004; Koch and Kiefer, 2005). To achieve a cross-species comparison, segregating AFLP traits were isolated, cloned and sequenced. This technique was used for molecular markers forming the linkage group of the putative *Spe* locus.

Materials and methods

Plant material

Already in the 1980s the genus *Capsella* has been predicted to be a valuable model for evolutionary studies (Hurka, 1984) and

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