Morphological and Anatomical Aspects of Petaloidy in the Carrot
(Daucus carota L.)

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Abstract. One type of male sterility in carrots is expressed as the change of anthers to petaloid structures. Different shapes of petaloids were observed. According to the degree of petaloidy, they were filamentous, spoon-shaped, incomplete and complete. In most cases the 5 transformed stamens of a single flower exhibited the same shape, although in others some variability existed. Serial sections of normal and petaloid stamens revealed anticlinal cell division of the epidermal cell layer early in stamen primordia development to be associated with petaloidy. In one of the lots the anthers were not completely transformed and in this case there was an inverse relationship between the degree of petaloidy and anther locule development. In anthers where pollen grains dehisced, some were viable and germinable.

Introduction

The term petaloidy refers to the transformation of any of the flower parts into a petal-like structure. In some cases the pistil or the calyx is transformed but the stamen is the organ which most commonly becomes petaloid (3). Its occurrence in stamens renders the flower male sterile and makes it of value in hybrid seed production.

Petaloidy was observed in wild carrots in 1953, and since then it has been used in carrot breeding programs. Its inheritance has been determined to be a result of the interaction of a cytoplasmic factor and at least 3 dominant genes (5). The expression of petaloidy was reported to be variable and ranged from strap-like to complete petaloids. Cross sections in young buds showed the leaf-like formation of the transformed stamen early in floral development (5).

This paper reports the range of petaloidy expression morphologically and anatomically and the relationship between the two. Another objective of this paper was to investigate the viability and germinability of pollen grains produced by one of the lots (2886) used in this study.

Materials and Methods

Several inbred lines and F₁ crosses of carrots known to show petaloid anthers were used. One of these, a hybrid designated as 2886, was included because it had been observed to exhibit variable expression of petaloidy. The normal cultivar 'Royal Chantenay' was also included. Seeds were sown at the Freeville farm near

Fig. 1-7. Close up of normal and petaloid carrot flowers.

Fig. 1. Normal flower showing 5 stamens alternating with 5 petals (X 15).

Fig. 2. Complete petaloid flower (X 25).

Fig. 3. A petaloid flower showing filamentous structures (X 15).

Fig. 4. A flower with spoon-shaped petaloids (X 15).

Fig. 5. A flower showing complete petaloidy of the anther and incomplete transformation of the filament (X 15).

Fig. 6. Variability of the shape of the petaloids within one flower (X 15).

Fig. 7. A flower from the lot 2886 showing different degrees of petaloidy and incomplete petaloidy of the anthers. One of the stamens looks normal (X 15).

Fig. 8-17. Cross sections in normal and petaloid flowers.
Ithaca in early June 1966 and 1967. After digging, the roots were placed in cold storage at 40°F for at least 7 weeks to induce flowering. They were then potted and grown under favorable greenhouse conditions until flowering.

The carrot flowers were observed at anthesis under a dissecting microscope ($\times 10$), which permitted accurate classification of the morphology of the petaloids. Young umbels, umbellets and individual flowers were fixed in formalin-acetic acid-alcohol (FAA). Dehydration and embedding of the tissue in paraffin followed fixation (2). Serial sections of 8–12 μ thickness were stained using Heidenhains iron alum hematoxylin and saffrin (1) or saffrin and fast green.

To test pollen viability, tetrazolium salt 3(4,5-di-

methyl thiazolyl 1–2) 2, 5-diphenyl tetrazolium bromide (MTT) was used (4). For pollen germination, different combinations of 0–70% sucrose solution and 0–100 ppm boric acid were tested.

**RESULTS AND DISCUSSION**

**Morphology of normal and petaloid flowers.** A normal carrot flower has 5 stamens with cylindrical filaments (Fig. 1). In complete transformation of the stamens, the petaloids become like another whorl of petals but smaller in size (Fig. 2). The color of petaloids ranges from white to green depending on the breeding line. Other shapes or degrees of petaloidy between the normal and the complete were observed. The petaloids may look filamentous, lacking the anthers (Fig. 3); or transformation of the anther but not the filament may take place leading to a spoon-shaped petaloid i.e. a leafy appearance (Fig. 4). The filamentous shape was the least degree of petaloidy observed. Morphologically the spoon-like structure supports Worsdell’s concept (6) that the petaloid is a leaf, the anther being the lamina or the blade and the filament the petiole. The next degree was similar to the previous category except that the filament was partially petaloid (Fig. 5). Sometimes the tips of the petaloids were lobed, especially in the white petal lots.

Although in most cases all the transformed stamens of a single flower looked the same, different shapes may occur within the same flower. Fig. 6 shows a flower with 2 spoon-shaped petaloids and an incomplete one. This was not characteristic for a particular position of the flower in the umbellet or for the order of the umbel.

The petaloid structures described above did not show any sign of pollen production. However, plants of the lot 2886 produced petaloids with yellowish anther tips. Fig. 7 illustrates a representative flower from this lot showing different degrees of petaloidy with anthers not being completely petaloid. One of the stamens looks normal and has a cylindrical filament with pollen grains dehiscing from its anther.

**Anatomical studies.** A cross section in a normal flower at anthesis showed 5 anthers alternating with 5 petals (Fig. 8). Each anther had 4 locules containing pollen grains. The cylindrical filament is shown between the 2 anther lobes (Fig. 9). The outer layer is the epidermis followed by the ground tissue which contains an oil duct and one vascular bundle. At an earlier stage of stamen development, a cross section demonstrated that the anther locule shape was distinctive when the pollen microsporocytes were at the quartet stage (Fig. 10). This indicated earlier determination of the stamen shape.

A cross section of a complete petaloid flower showed 5 transformed stamens around the 2 styles alternating with true petals which were larger in size (Fig. 11). With higher magnification of the petaloids, a leaf-like structure with one central vascular bundle was observed (Fig. 12). The mesophyll-like layer was darkly stained and compressed between the extended epidermal cell layer. In a very young umbel petaloids were distinguished by their leaf-like shape in a cross section (Fig. 13). It was suggested from this observation that petaloidy was manifested early in flower development. The leafy shape of a petaloid in a cross section differed from a normal filament by the extension of the epidermal cell layer as a result of cell division at the sides. Hence, it was assumed that petaloidy was due to an increase in the anticlinal cell division of the epidermal layer at an early stage of development of stamen primordia.

Cross sections were made in petaloids of the lot 2886 in order to study pollen development and petaloidy. Anther locules were compact, reduced to 2 instead of 4, and contained darkly stained material in place of pollen grains (Fig. 14). A greater degree of petaloidy was manifested along with less differentiation of anther locules (Fig. 15). It appeared that a decrease in size of the anther locule was the result of the formation of a petal-like anther containing only small vacuolar spaces (Fig. 16). An inverse relationship between anther locule development and petaloidy was observed (Fig. 14–16).

**Pollen viability and germination tests.** The viability of pollen grains produced from lot 2886 was tested using tetrazolium salt MTT. Some of the dehisced pollen grains stained purple indicating that they were viable, but the majority of them did not stain and some were shrivelled (Fig. 17). In the germination test, some of the pollen grains germinated on a medium containing 45% sucrose and 50 ppm boric acid.

In view of the inheritance of petaloidy, the previous results could be explained if it was assumed that lot 2886 has one of the 3 genes in a recessive condition leading to some pollen fertility. Other genes interact with the cytoplasmic factor to promote petaloidy. The inverse relationship between petaloidy and anther locule development indicated that earlier action of the recessive
gene leads to normal stamen formation without petaloidy. However, if the recessive gene and the other genes with the cytoplasmic factor exerted their effect at the same time, different degrees of anther locule development result.

Literature Cited