LETTER TO THE EDITOR

Goethe, Sex, and Flower Genes

Although I appreciate the excellent series of papers on plant reproduction in the October 1993 special issue of The Plant Cell, I would, nevertheless, take exception to some of the basic comments on flower morphology by Coen and Carpenter (1993) in their otherwise informative article.

The authors argue, with Goethe (1790), that flowers and shoots are fundamentally equivalent, that is, that the different parts of a flower (sepals, petals, stamens, carpels) are equivalent to the leaves of a shoot. Because internodes in the flower are "so short as to be barely visible" (p. 1175) or, in contrast to floricaula, "undetectable" (p. 1176), a shortening of the internodes is envisioned. The phyllotaxy of floral organs is usually different from that of leaves, and flower growth is determinate (both apically and laterally) instead of indeterminate. Thus, organ identity, internode length, phyllotaxy, and determinacy have all been changed. These changes are thought to be "simply different modifications of a common growth plan," produced by "different permutations of a few key features of plant growth" (p. 1175).

In positing this equivalence theory of the flower and stem, the authors have, however, not considered the most important aspect of flower morphology: sexuality or sexual reproduction, i.e., that aspect of the flower for which it exists at all. In fact, Goethe, seeing that his theory ("everything is leaf") did not correspond to the sexual aspect of plant reproduction, later denied sexuality in plants (Goethe, 1820), together with the botanists Schelver (1812) and Henschel (1820), although the sexual functions of the stamens and carpels had been shown conclusively by Camerarius (1694), Linné (1735), Körreuter (1761–1786), and, finally, Sprengel (1783). One should also keep in mind that Goethe's statements were made in the tradition of Platonic idealism and had no phylogenetic implications (Goethe speaks repeatedly of the "inner identity" of flowers and shoots and the "identity of all plant parts").

However, there is no equivalence of the flower and shoot concerning sexual reproductive functions. Kamalay and Goldberg (1980, 1984) showed that "both the anther and the ovary contain approximately 10,000 diverse mRNAs that are not detectable in heterologous organ system mRNA or nuclear RNA populations" (Drews and Goldberg, 1989, p. 259). Several other authors have obtained similar results (Willing and Mascarenhas, 1984; Smith et al., 1989; Koltunow et al., 1990). And, beginning with Sommer et al. (1990) and Yanofsky et al. (1990), several flower morphology genes have been cloned and sequenced that are expressed only in the flower and nowhere else.

Whatever the exact number of special regulatory and target sequences that are involved in and expressed during flower development only, the independent results of several authors that a large number of genes are expressed solely in the flower clearly disproves the simple equivalence of flowers and shoots claimed by Goethe and his followers.

In contrast to the equivalence theory (and bearing in mind that from the functional point of view, all the flower structures finally serve, or are produced for, the aim of sexual reproduction and propagation), one could argue that during flower development most of the typical characters of the vegetative shoot are more or less progressively lost, being replaced by the new genetic programs and corresponding features for sexual reproduction. In this respect, the flower is not equivalent to, but essentially different from, and definitely more than, the shoot. Sexuality is the reason why the meristem structure, organ identity, internode length, phyllotaxy, and determinacy of the flower are all so different from those of the shoot. Let it be emphasized again that entirely different genetic programs are switched on during this stage of development. Or, speaking allegorically, a new chapter with a new topic is opened, a new movement of the developmental symphony has begun.

This does not exclude, of course, the possibility that the introductory phase of flower development (sepals and petals) consists largely of the repetition of already known genetic programs (Drews et al., 1992), transformed by a minority of new regulatory gene functions for special developmental and morphological tasks. The main part of flower development, however, is made up of the organs for sexual reproduction, i.e., the stamens and carpels, so that the large majority of the new programs is expressed here.

Although many researchers have felt that mutants transforming floral organs into leaflike structures seem at first glance to imply that flowers and leaves are in fact equivalent, the following homeotic examples will reveal just the opposite. In the well-known plena mutants (see, for example, Masters, 1869), stamens are replaced by petals, and carpels by sepals, followed by further petaloid structures in the central part of the flower. Because the MADS-box gene PLENA in Antirrhinum (and the homologous gene AGAMOUS in Arabidopsis) is essential for turning on the complex genetic programs for stamen and carpel formation, its loss of function also implies the loss of these sex organs, and the simpler petal and sepal programs are continued into the two inner flower whorls—that is, the field where the PLENA gene is normally expressed (Yanofsky et al., 1990; Bradley et al., 1993).

Now, does this loss of PLENA gene function, with the accompanying loss of the thousands of additional diverse mRNAs for sex organ formation, imply that the genetic programs for leaves, stamens, and carpels are all equivalent? Sattler (1986, p. 1607) gives the answer for the homeotic plena change by the following
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analogous illustration: "If a botanist in a biology department is replaced by a zoologist (as too often happens), the latter is not a transformed botanist simply because his predecessor was a botanist; he only occupies the same position. From the sameness of position, it does not follow that members occupying it are also essentially the same; they may be similar or very different." And in the case of \textit{plena}, the members (floral organs) are, in fact, very different: instead of sex organs (including the temperature-sensitive allele \textit{daff-101}) are the atavistic gene sequences of flowering plants. The same can probably be said of the alleles of the homologous \textit{APETALA3} gene in Arabidopsis (Jack et al., 1992). The substitution of a late developmental program by an earlier one does not necessarily prove the equivalence of both. Although the bulk of diverse mRNAs is equivalent in leaves and petals, the different governing regulatory systems and the corresponding qualitative and quantitative mRNA differences of these distinct organ classes are obviously not. Because of organ-specific gene expression at the RNA and/or protein levels (Jack et al., 1994), targeted gene tagging can often concentrate on special flower (or other) characteristics (see, for example, Lönnig and Huijser, 1994).

Furthermore, the null alleles of \textit{DEF} and \textit{APETALA3} display not only sepalas instead of petals but also carpels in place of stamens. As far as I am aware, it has never been proposed from this that stamens are "derived" from carpels.

In the often quoted case of Goethe's "example of a rose grown through" (Goethe, 1790; Weberling, 1989) — a malformation in which flower development is stopped shortly before, or at the beginning of, another development and shoot growth is resumed — the flower programs are switched off at this developmental stage and the stem programs are turned on again. Asserting the equivalence of both programs for this reason would be simply illogical.

In short, the expression of special shoot features in abnormal flowers shows only that such shoot programs (or parts of them) were turned on at the wrong time and at the wrong place. They do not prove the equivalence of the genetic programs for stems and flowers any more than the accidental mixing of two different computer text programs on biology and poetry proves their equivalence, although the same letters, words, and basic grammar may be involved (the words may be identical, but the message is not).

Beginning with systematic research by Payer (1857), many other authors have basically come to the same conclusion (involving also the telome theory, in which both stamens and integuments are thought to derive not from leaves but from telomes, as well as the sui generis theories of flower structures and many further ideas and arguments that cannot be discussed here). Abridged histories of the different views are given by Meeuse (1987) and Lercy (1993).

Molecular genetics has \textit{definitely disproved} Goethe's idea of the equivalence of flowers and shoots by showing that anthers and ovaries express thousands of diverse mRNAs that are not detectable in heterologous organ systems and that certain specific cloned genes are expressed only in the flower and not in the shoot (or vice versa). Although "simply different modifications of a common growth plan" may be envisioned to be involved in some of the changes between the stem and the flower, the basic cause for all the differences in meristem structure, floral axis anatomy, organ identity, internode length, phyllotaxy, and determinacy is sexual reproduction having no equivalence in the stem.

Because misconceptions on this topic are very widespread, I think that publication and discussion of this letter would help plant science to clarify these points.

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