Modelling the plant, Goethe and molecular genetics

> **“In this way chemistry has exactly observed the changes of the smallest particles and their composition, and her last important activity and accuracy gives her the right to assert a claim on the uncovering of organic natures.**
>
> **From all these … it is easy to see that one has reason to order all our abilities, when we truly want to understand those secrecy’s, that we are urged to use all inner and outer tools, and to use all benefits when we venture this always endless work. Even a certain kind of one-sidedness is for the whole not detrimental, everyone can hold his way for the best one, presumed he planes, and cleans his way, so that the following people can go this way easily.” Goethe** (1964 pp. 138-139[1])

Goethe’s Metamorphosis of Plants in the translation of Agnes Arber (1946) has become the most cited scientific work of the 18.th century by plant geneticists in the past decade. There are at least two reasons for this interest (Coen 2000). Goethe recommended the use of mutated plants to unveil the secrets of normal plant development and he formulated the hypothesis that floral organs are modified leaves and leaves modified floral organs. Goethe’s statement that “leaves are modified floral organs” although is difficult to reconcile with the fact that vegetative leaves originate before floral organs both ontogenetically and phylogenetically. Molecular biologists are specialists in producing abnormal plants, they could not do their job without mutated plants and they have experimentally shown that floral organs can be replaced by leaves and leaves by petals, stamens or carpels (Bowman et al. 1991, Goto at al. 2001, Theissen and Saedler 2001, Pruitt et al. 2003).

An investigation of Goethe’s work on the metamorphosis of plants, also considering his estate (Goethe, 1964 and 1977), combining with results of molecular genetics, brings new aspects in the discussion concerning the modelling of the plant. This article deals with embryogenesis and Goethe’s ‘organic disunion’, the body plan of the seedling, the transition of the vegetative plant into the generative plant, the ABC(E) model, partial homology of floral organs with leaves, the ‘separation of the sexes’, phytomers, the difference between metamorphosis and homeosis. Results of molecular genetics not only confirm the hypothesis of Goethe, of the leafy nature of the floral organs, they also show that the ground state of the carpel is the vegetative leaf with its accompanying bud(s). The stamen has not the same ground state as the carpel; here we find characteristics of the leaf and the root.

The reason why Goethe’s morphological publications and estate are still of importance for today’s science is his concept of metamorphosis. His determinations of morphological relationships between organs and organ parts are today at first of historical interest. The enormous progress in determining morphological relationships between organs in the past two centuries can not be overlooked. Goethe (1790) compares for example in §70 the stamen as the male organ with the pistil as the female organ and not with the carpel as we do today.

Goethe wanted to know the rules for the ever changing forms of the plants. His ‘Metamorphose’ deals mainly but not only with the transformation of leaves. In §113 he compares the successive vegetative propagation from node to node with the generative propagation, which happens at once. Other essays and outlines also deal with the relationship between vegetative and generative propagation (1964, p. 57), with the metamer construction of the plant body (1964, p. 57) and with the relationship between the root and the shoot (1964, p.133).

---

[1] Translation: Peer Schilperoord

Goethe's metamorphosis of the vegetative plant and of the leaves and his hypothesis of the purification of the saps to explain leaf metamorphosis has attracted attention by molecular biologists. The hypothesis, that metamorphosis depends on the purification of the sap, has been disproven. According to this hypothesis carpels could not be established before stamens or petals before sepals and so on. Many mutant phenotypes show, that the establishment of a special organ type is independent of the adjacent type (Bowman, 1994).

Goethe and the ABC model

Goethe is often quoted in connection with the ABC model (Bowman et al. 1991) (Figure 1 and 9). This model predicts and explains some (not all[2]) phenotypes of A, B and C class mutant flowers. Weigel and Meyerowitz (1994) wrote: "Goethe had proposed that floral organs represent modified leaves, suggesting that a vegetative leaf is the ground state of the floral organs. This has been confirmed by double and triple mutants. … In triple mutants that lack A, B, and C activities, all floral organs resemble leaves." The triple mutant shown was ap2-1 pi-1 ag-1 with green leaf like organs, covered by branched hairs (Fig. 2). But triple mutants show often still features of both carpels (stigmatic tissue, fusion of organs along their margins and ovules) and leaves (stellate trichomes and stipules) (Goto et al. 2001). The C class gene AGAMOUS does not fully specify carpel identity. Mutants of CRABS CLAW and SPATULA in an ABC triple mutant background reduce the amount and type of carpel tissues that develop (Fig. 3) (Alvarez and Smyth, 1999).

Figure 2. Ground state of floral organs. Triple mutant ap2-1 pi-1 ag-1. (Bowman et. al. 1991)

Figure 1. The ABC Model (1991) is based on ap2 mutant phenotypes. AP2 suppresses AG, AG suppresses AP1. The ABC Model: at the left the genes on which the model is based, at the right the generalised model (A = AP1, AP2, B = AP3, PI and C = AG)

The ABC model predicts the replacement of floral organs by green leaves. It took after the formulation of the ABC model a decade of research to replace green leaves by floral organs. Experiments with the ectopic expression of the ABC genes failed to convert leaves in floral organs. First the ectopic expression of ABC genes in combination with the ectopic expression of SEPALLATA genes turned leaves into floral organs (Honma and Goto, 2001). Leaves are converted in petaloid organs by ectopic expression of PI-AP3-AP1 und PI-AP3-SEP3 (Honma and Goto, 2001) (Figure 4) in petals by ectopic expression of AP1-AP3-PI-SEP3 (Pelaz et al. 2001) in staminoid organs by ectopic expression of PI-AP3-SEP3-AG and in car-

---

[2] See: "the transition from the vegetative in flowering plant".

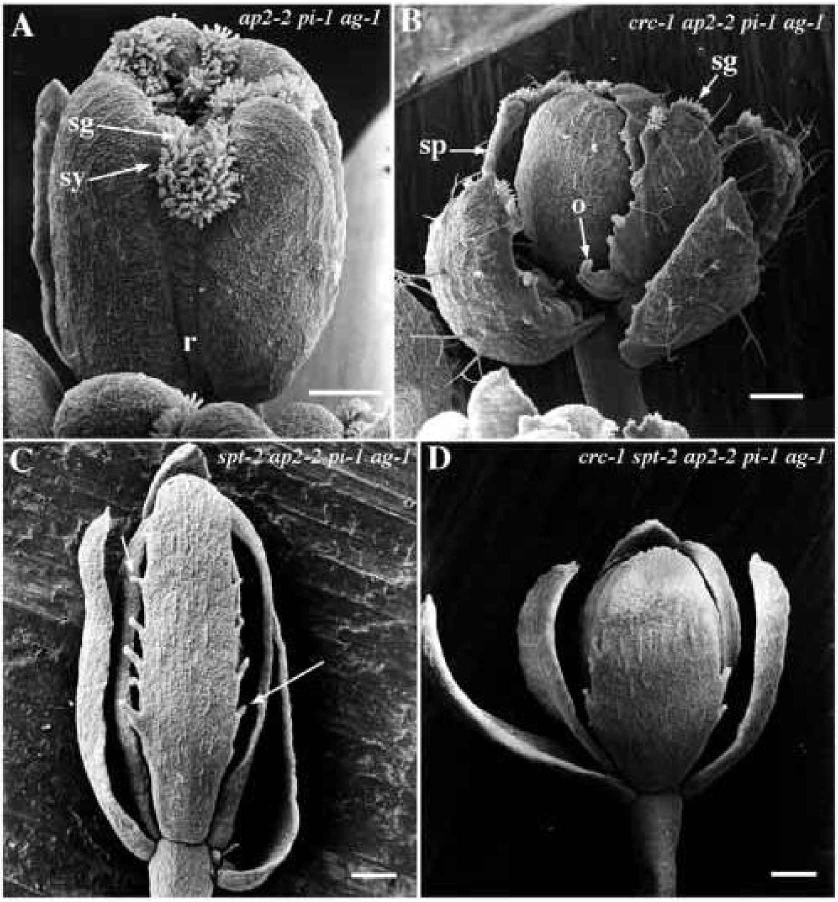

Figure 3. Loss of carpelloid properties in *ap2-2 pi-1 ag-1* (ABC) triple mutant flowers consequent upon progressively introducing the *crc-1* and *spt-2* mutations. (A) *ap2-2 pi-1 ag-1* triple mutant. Organs in this flower are fused along their edges where replum (r) cells arise, and style (sy) and stigma (sg) development is confined to the unfused commissural positions. Internally, both the septum, including a functional transmitting tract, and ovules may arise. (B) *crc-1 ap2-2 pi-1 ag-1* quadruple mutant. Organs are now more ovate although still hood-shaped, particularly at their apex. Sporadic development of stigma (sg), septal tissue (sp) and ovule-like primordia (o) may occur along their edges. (C) *spt-2 ap2-2 pi-1 ag-1* quadruple mutant. Organs are linear with parallel edges, and have lost any hood-like shape. There is no sign of style, stigma or septal development. Marginal outgrowths may arise (arrows), and these occasionally develop some ovule-like properties. (D) *crc-1 spt-2 ap2-2 pi-1 ag-1* pentuple mutant. The organs are now almost completely vegetative in appearance. They are ovate and flat, with very few marginal outgrowths. Scale bars: 250 µm. (Alvarez and Smyth, 1999)

pelloid organs by ectopic expression of AG-SEP3 (Goto et al. 2001). The conversion of leaves into sepals has until yet not been reported. The better understanding of the SEP genes let to the formulation of the protein based quartet model (Figure 5 and 10) which replaced the gene based ABC model.

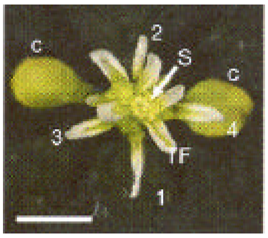

Figure 4. Three week-old 35S::PI; 35S::AP3; 35S::SEP3 plant. Cotyledons are rather normal, but true leaves are transformed into petaloid organs. Numbers show the order of leaf development. S, Stamens; TF, terminal flower. (Honma and Goto, 2001)

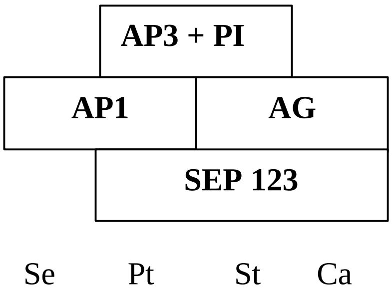

Figure 5. The quartet model (ABC 2001) is based on AP1 and the formation of tetramers. Petals arise when the four gene products of AP3, PI, AP1 and SEP form a tetramer; stamens arise, when the products of AP3, PI, AG and SEP form a tetramer.

The statement that floral organs are modified leaves overestimates the role of the leaf, for floral organs are more then leaves. The statement, that molecular genetics experimentally proved Goethe's hypothesis of the *leafy nature* of floral organs, is a more precise formulation. The transition from the vegetative into the reproductive phase is a complex one. Completely new organs like pollen grains, ovules and embryo sacs embedded in leafy structures arise, the internodes become very short, lateral shoots and roots do not arise and the terminal growth is left off.

Goethe concluded "flowers which develop from lateral buds are to be regarded as entire plants, which are set in the mother plant, as the mother plant is set in the earth" (Goethe, 1790 §95, Coen and Carpenter 1993). What kind of modifications take place, can we look at the flower as a modified vegetative plant? We have, answering this question, to describe the relationships between the organs of the vegetative plant and compare this description with the relationships between the organs of the generative plant. Helpful are those gene mutations, which both influence the phenotype of the vegetative as well of the generative parts.

Although Goethe was well known to famous morphologists like Agnes Arber and Wilhelm Troll, both were editors of Goethe's metamorphosis (1946, 1926), they did not recognise the importance of Goethe's idea of 'organic disunion' (1964, p. 133), which is the morphological key to understand relationships between organs which are each other so completely dissimilar as the shoot and the root or stamens and carpels (Schilperoord, 1997, 2000).

The vegetative plant

Embryogenesis and the re-examination of the traditional morphological concept of the basic organs

Shoot and root systems of land plants carry out complementary functions. Shoot axis and leaves arise both from the shoot apical meristem. The shoot axis arises continually, the leaves successively. The leaves are especially exposed to the surrounding light and air. The shoot axis connects the leaves and the shoot apical meristem to the root.

When we look at the root in the same way as we have looked at the shoot, we have to discern an organ which is especially exposed to the surrounding earth and water, and an organ which connects those exposed parts and the root apical meristem to the shoot. The parts which are especially closely connected to the surrounding earth are the central root cap, the lateral root cap, the epidermis with the root hairs and the rhizoderm. These parts together form the organ which is complementary to the leaves. The polarity of the shoot apical meristem and the root apical meristem is reflected in the polarity of the shoot axis and the root axis and in the polarity of the leaves and an organ - what I have called the root organ (Schilperoord, 1997) - which arises and decays continually.

Traditional morphology distinguishes between root, shoot axis and leaves, the so called basic organs (Troll 1967, Sitte 1991). This traditional concept of the three basic organs is not very well founded. "The corm as a rooted shoot is build by the three basic organs axis, leaf and root. The basic organs cannot be homologised with each other and they exercise basic functions." One reason to look at the root as an organ of the same class as the shoot axis and the leaf is surely that the parts of the root which are closely connected with the surrounding earth and water do not take themselves very much off from the axis. Another reason is the restrained idea we have of the shape of an organ. When we accept the idea, that an organ must not have a fixed shape, and that different tissues of the organ can arise and decay successively, then we have no problem to distinguish two organs by studying the root.

Do mutant phenotypes support the idea to distinguish morphologically first between the root and the shoot pole and secondly distinguish between the shoot axis and the leaf as parts of the shoot and between the root axis and the root organ as parts of the root?
Normal Embryogenesis can be disrupted in two ways. The development of the radial pattern and of the apical basal pattern can become irregular (Jürgens, 1994). The irregular development of the apical basal pattern is here of special interest. The apical basal pattern can already be disrupted during the development of the zygote in the GNOM mutant. The orientation of the first zygotic cell division is randomized in gnom mutant embryos and the most severely affected embryos develop as ‘green balls’: underneath the surface layer of epidermis, a sphere of ground tissue surrounds a central ‘cloud’ of vascular cells (Mayer, et al. 1991). A weaker phenotype as the ‘ball-shaped’ seedling is the ‘oblong’ seedling which seems to have an axis as indicated not only by its shape but also by the distribution of vascular cells which are scattered along the axis (Figure 6) (Mayer et al., 1993, Schiefelbein et al., 1994).

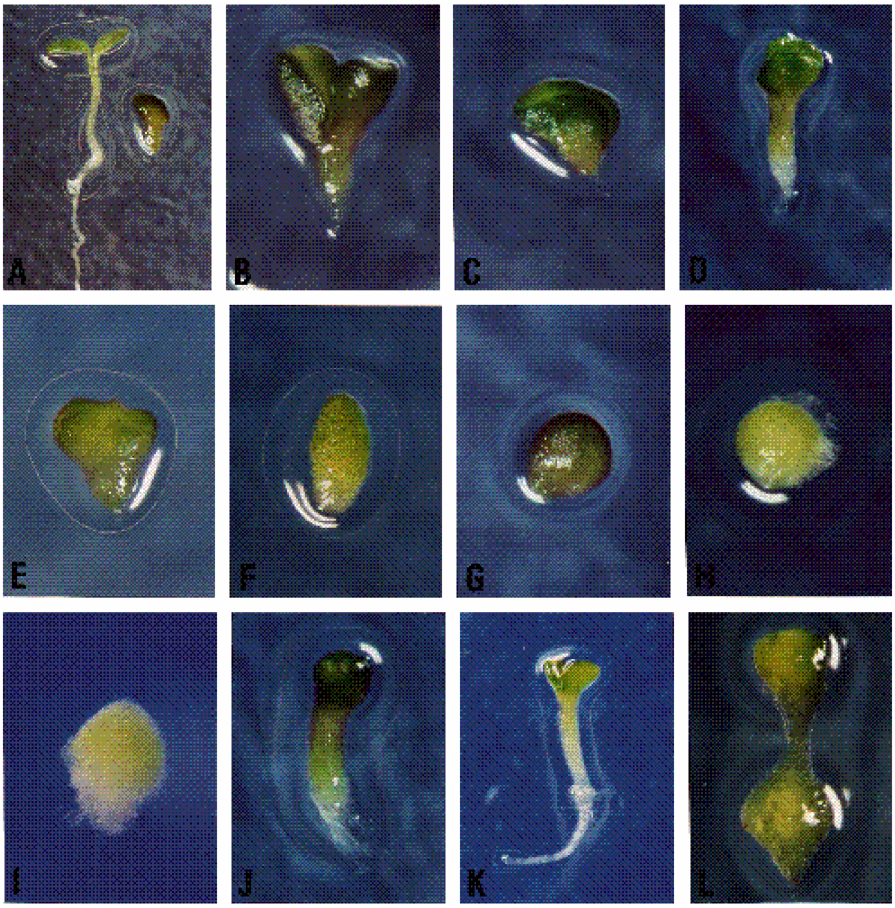

Figure 6. Phenotypes of *gnom* mutant seedlings. (A) Wild-type seedling on the left and ‘cone-shaped’ *gnom* mutant seedling on the right; (B-D) ‘cone-shaped’; (E,F) ‘oblong’; (G,H) ‘ball-shaped’; (I-K) ‘root’ phenotypes: (I) ‘oblong’ type, (J) ‘cone-shaped’, (K) ‘weak’ phenotype of *gn*4-13/*gn*U87 trans-heterozygote; (L) ‘double *gnom*’.
Mayer et al. 1993.

Mutants with broad deletions of seedling regions originating after the first cell division are the monopteros, gurke and fackel mutants (Figure 7) (Jürgens 1994). The monopteros mutant seedlings lack basal body structures, radicle and root meristem cannot be developed and the hypocotyl can also be missing (Berleth and Jürgens, 1993). The gurke mutants lack cotyledons and shoot meristem and in the fackel seedlings appear the cotyledons to be directly attached to the root without any indication of an intervening hypocotyl (Jürgens 1994). In Arabidopsis, the apical - basal axis is partitioned from early on into three major regions: apical, central and basal, within the central region, a radial pattern of concentric tissue layers is established successively from the periphery to the centre (Torres-Ruiz et al., 1996).

The first step in embryogenesis is the establishment of a linear polarised proembryo. The next developmental stage, the ‘globular’ stage, shows the spatial separation of the developing root

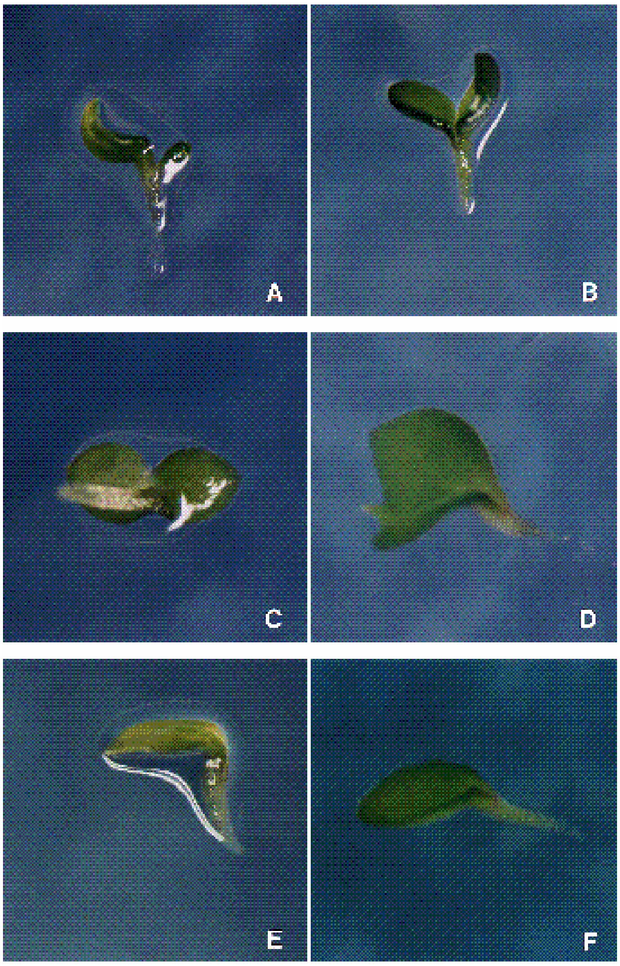

Figure 7. Spatial arrangement of cotyledons in *mp* mutant seedlings. (A, B) Normal position of the cotyledons which can differ in size. (C, D) Intermediate types of cotyledon fusions, ranging from angles slightly less than 180° between the cotyledon axes (C) to almost completely fused cotyledons (D). (E, F) Seedlings with a single cotyledon) which can be oriented differently relative to the 'basal peg'. Mutant alleles: *mpT1* (AC, E, F); *mpT370* (D). Berleth and Jürgens, 1993.

and shoot apical meristems (Long and Barton, 1998). In the central part, this connects both developing meristems, starts the differentiation of the protoderm, procambium and subepidermal ground tissue. This central part includes as well cell lineages which contribute to the shoot, for example to the abaxial site of the cotyledons, as to parts of the root, for example to the first root hairs (Scheres et al., 1994). In the 'heart' stage are at the shoot pole the first two cotyledonal leaves incepted and at the root pole is the root cap formation initiated (Kaplan and Cooke, 1997). According to Long and Barton (1998) is the shoot apical meristem completely established and anatomically detectable at the 'walking stick' stage.

Another mutant, the TOPLESS mutant (Long et al., 2002) shows in its strong version a completely differentiated root and a transformation of the shoot pole into another root (Figure 8). The result is a seedling with two roots joined at the base and no hypocotyl, cotyle-

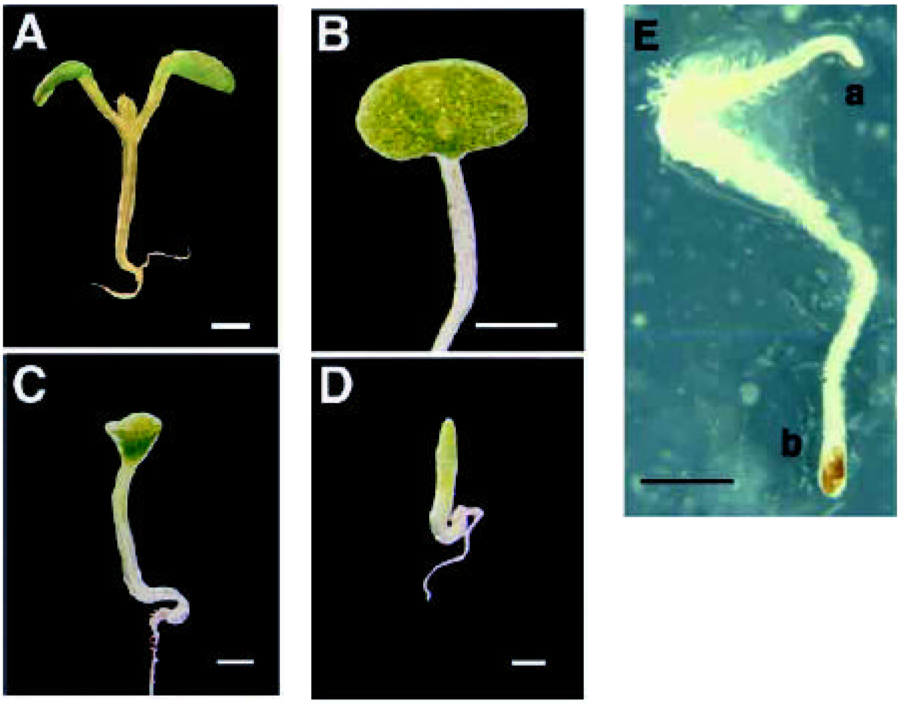

Figure 8. Topless. Representative phenotypes of seedlings homozygous for the *tpl-1* mutation. (A) Wild-type seedling. (B) *tpl-1* homozygote that has developed a single cotyledon and lacks a shoot apical meristem. (C) *tpl-1* homozygotes that has developed a cup-shaped cotyledon and no shoot apical meristem. (D) *tpl-1* homozygote that has developed with no detectable cotyledon tissue or shoot apical meristem. (E) *tpl-1* homozygote that has developed both an apical (a) and a basal (b) root. Scale bars:
1 mm. (Long et al. 2002)

dons or shoot apical meristem. The topless embryos fail to express markers for the shoot apical meristem (SHOOT MERISTEMLESS and UNUSUAL FLORAL ORGANS) and for the hypocotyl (KNAT1).

The partitioning of the vegetative plant in root, shoot axis and leaves does not reflect the equivalency of the root and the shoot pole in embryogenesis. The results of molecular genetics should for morphologists be an occasion to re-examine the concept of the basic organs of the vegetative plant. The morphological concept of the basic organs should reflect the process of embryogenesis and the functional aspects of both the root and the shoot. This is the case when we discern between leaf, shoot axis, root organ and root axis as basic organs (Schilperoord 1997, 2000).

Embryogenesis and Goethe's 'organic disunion'

Goethe has written an outline 'Versuche zur Methode der Botanik' (essay on the method of botany) (1964), which is found in his estate. In this essay he introduces the idea of organic disunion in chapter IV. In Chapter III he wrote about organic unity.

> << IV Organic disunion.
> Before, we looked at the plant as a unity. We can see the empirical unity with our eyes. It arises by the association of many different parts of the greatest variety as an apparent individual. A one year old completed plant torn out. Ideal unity: When these different parts are thought to have arisen from an ideal body, and have developed sequentially. From the very beginning we have to consider this ideal body as simple as possible, and to look at it as disunited, for without the process of disuniting of an entity, a third one cannot develop.
> [...]
> Germ of the root and the leaf. Both are originally unified with each other, yes one cannot be thought without the other. They are each other opposite from the beginning too...>> (1964, p. 134).

We see here, that Goethe considers the first step in the development of the plant is the process of organic disunion and that this idea has been confirmed by the results of analyzing abnormally grown embryos.

Goethe discerns by using the adjective organic between inorganic and organic disunion. In the same sense we can use the adjective organic in combination with polarity. The term polarity has been used in morphology only in a positional sense. Can we use this term also in an organical, morphological sense?

The morphological polarity of the root and the shoot (Schilperoord, 1997) becomes visible in: 1. the circular configuration of the vascular strands in the centre of the root axis and a radial configuration of these strands in the periphery of the shoot axis with respectively endogenous and exogenous origin of lateral organs; 2. the so called root organ (root caps, root hairs, rhizoderm) arises and decays continually and has only one form. Leaves arise successively, they have different forms, and the leaf rests intact.

At the end of the chapter on organic disunion Goethe points out, that when we have the process of organic disunion at the beginning of plant development, we will find this disunion also in other parts of the plant. The separation of the sexes is for Goethe the summit of organic disunion (1964, p. 134).

Vegetative growth and phytomers

It is typical for the vegetative plant, that it repeats equal parts. Goethe describes this fact in 113: "When we study growth, we see that the plant succeeds from node to node, from leaf to leaf, and that also by sprouting a kind of propagation happens, which is different from the reproduction by the flower and the fruit, for she takes place successively, she shows itself as a series of single developmental steps." This basic unit of the vegetative plant is often called phyton, phytomer or metamer. I here use the definition of James White (1984); a phytomer or metamer includes leaf, leaf node, and the internode beneath the node, root buds and shoot buds. The metameric organisation of the plant is obvious and commonly accepted. Talbert et al. (1995) for example distinguishes between vegetative and reproductive phytomers. The concept of serial homology of leaves and floral organs is based on the phytomer concept.

The transition from the vegetative plant into the flowering plant

The ground stage of the floral organ is not the vegetative leaf alone

"Flowers which develop from lateral buds are to be regarded as entire plants, which are set in the mother plant, as the mother plant is set in the earth" (Goethe, 1790). In comparing flowers to plants four key assertions need to be made.

First, the different parts of the flower (sepals, petals, stamens and carpels) are partially equivalent to the leaves of the shoot. Second, the organs of both shoot and flower are separated by internodes, but in the case of the flower these are so short as to be barely visible. Third, the organs of shoot and flower usually have a distinct phyllotaxy. Fourth, the indeterminate growth of the shoot and lateral branching is suppressed in the flower. Sexual propagation replaces vegetative propagation.

We can expect in the case of incomplete transformations: lateral branching, elongation of the internodes, leaves, a spiral phyllotaxy, indeterminate apical growth, and loss of floral organs or parts of floral organs.

The 1991 gene based "ABC model" (Figure 9) and the protein based "quartet model" (Figure 10) (Theißen 2001) are landmarks in recent biological research. The 1991 ABC model (Bowman et al., 1991, Pruitt et al., 2003) is based on AP2, AP3/PI and AG mutant phenotypes.

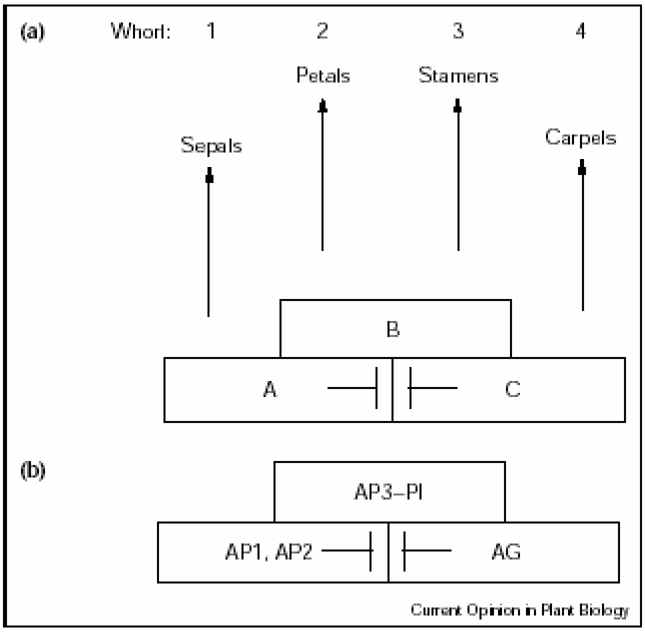

Figure 9. The **'classical ABC model'** for flower organ identity in *Arabidopsis.* **(a)** Floral organ identity is specified by homeotic functions A, B and C, which are each active in two adjacent whorls. A alone specifies sepals in whorl 1; the combined activities of A and B specify petals in whorl 2; B and C specify stamens in whorl 3; and C alone specifies carpels in whorl 4. The activities A and C are mutually antagonistic: A prevents the activity of C in whorls 1 and 2, and C prevents the activity of A in whorls 3 and 4. **(b)** The proteins providing the floral homeotic functions in *Arabidopsis.* Except AP2, all are MADS-domain proteins, which are expressed in the regions in which they specify organ identity. Antagonistic interactions are indicated by barred lines. A hyphen indicates heterodimer formation, a comma symbolises that the mode of interaction is unknown. Theissen, 2001

In the 2001 model (Theissen and Saedler, 2001, Pruitt et al., 2003) the role of AP1 (Irish and Sussex, 1990) is emphasized and for the conversion of leaves into petals (Honma and Goto, 2001) is AP1 the essential A-Class gene. It is an interesting point, that the ABC 1991 model could only have been formulated by considering AP2 mutant phenotypes only; it could not have been formulated using AP1 mutant phenotypes (Figure 11 and 12). Why is this a point of interest? Does it show that the ground state of the floral organs is the leave *and* its accompanying bud?

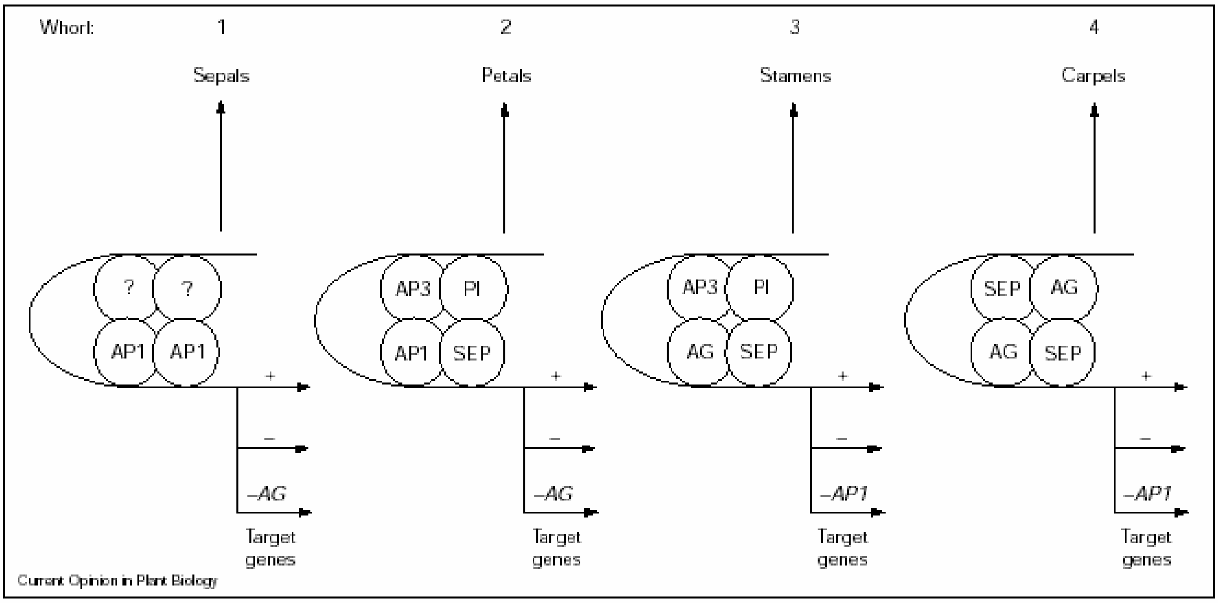

Figure 10. The **'quartet model'** of flower organ identity in *Arabidopsis.* The model suggests that four different combinations of four different floral homeotic proteins determine the identity of the four different floral organs. These protein complexes, which are assumed to represent transcription factors, may exert their function by specifically binding to the promoters of target genes, which they either activate (+) or repress (—) as appropriate for the development of the identities of the different floral organs. Binding probably occurs to pairs of diverse DNA sequence elements termed CArG-boxes (not highlighted here), which are brought into close vicinity by DNA bending. The antagonism between the A and C function in the 'classical ABC model' could be caused by the repression of *AG* gene expression by protein complexes that contain AP1. Similarly, complexes that contain AG repress the *AP1* gene. These interactions could, however, also be more indirect. Note that the exact structures of the multimeric complexes of MADS domain proteins controlling the identity of flower organs is still highly hypothetical. The model presented here is mainly intended as a working hypothesis for future research. (Theissen, 2001)

The phenotype of the ap1-ag double mutant (Irish and Sussex 1990) (Figure 11.3) is explained by the 2001 model, but not by the 1991 model. According to the 1991 model, one would expect staminoid petals but this mutant does not develop staminoid petals. Four bract-like first-whorl organs are developed with buds in their axils. Next, a variable number of green, leaf-like organs arise. The indeterminate nature of the ag-1 phenotype (figure 11.2) is still apparent in the ap1-1 ag-1 (figure 11.3) double mutants; the indeterminate nature of the ap1-1 phenotype (figure 11.1 and 12) is in the double mutant (figure 11.3) apparent too. The buds formed in the axils of the ap1-1 ag-1 bracts or leaf like organs repeat this indeterminate pattern of development. It can be expected that the triple mutant ap1 ap3/pi ag has the same phenotype as the double mutant ap1 ag. The combined loss-of-function of class A, B and C genes would not result in a transformation of all floral organs into leaves in the case of AP1.

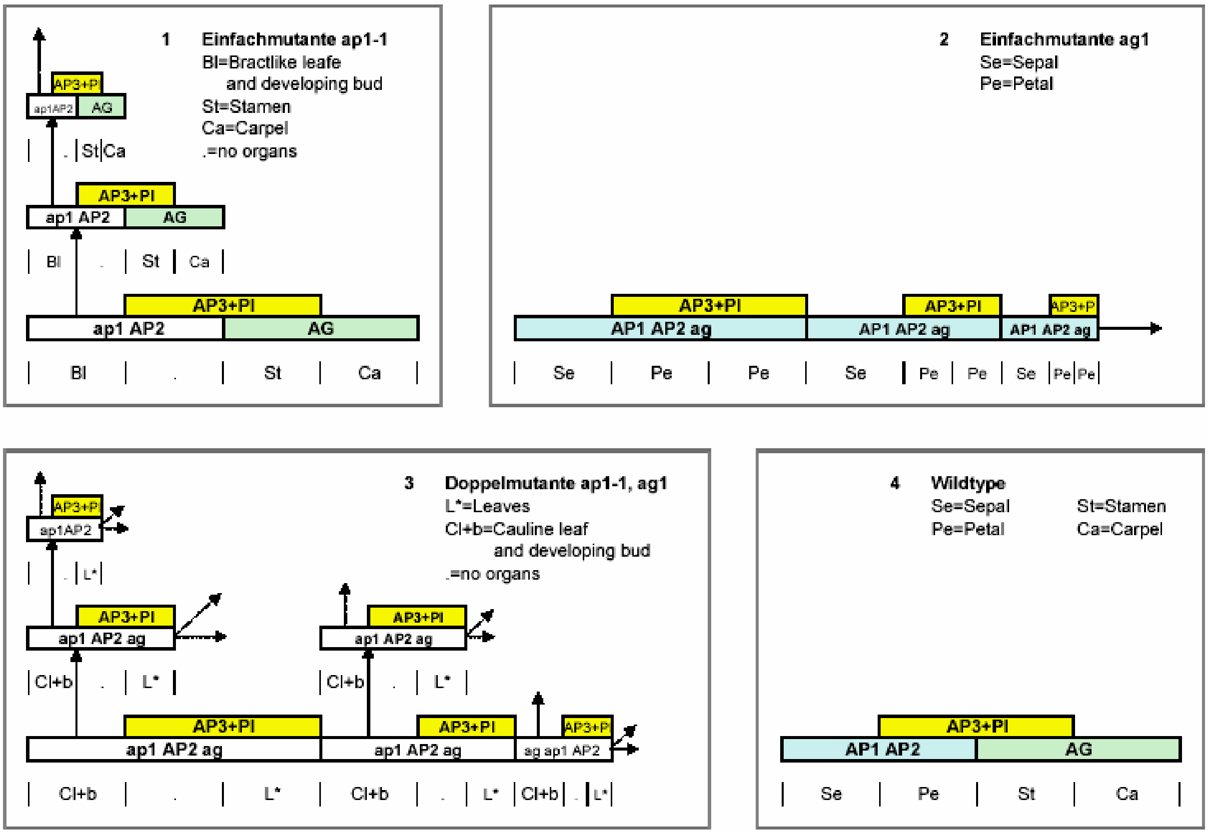

Figure 11. Phenotypes of ap1-1 and ag1 single mutant flowers; of ap1-1, ag1 double mutant flower and of wild type flower. Peer Schilperoord.

The connection between sepal development and inhibition of lateral bud formation is a very tight one. Both qualities have not been separated genetically after millions of mutant phenotypes.

The antagonistic behaviour of A and C class genes can be explained in a morphological sense when we look at the ap1, ap2 and the ag mutant flowers. The plant needs both AP1 and AG to terminate vegetative propagation in the form of axillary bud formation and ongoing apical organ initiation. In the ap1 mutant flower are sepals replaced by bract like structures with stipules and with buds in their axils. In the ap2 mutant flower is the suppression of AG in whorl one and two abolished, AG suppresses in this moment the establishment of AP1 in the first two whorls and the bracts and the lateral shoot apical meristem that would arise in the absence of AP1 are replaced by carpel like structures. In the double mutant ap2-2 ag-1 flowers (Bowman et al., 1991) are the medial first whorl organs often carpelloid leaves and in the fourth whorl develop carpelloid leaves too and is the growth indeterminate. In the fourth whorl of the wild type flower are those leaves and the indeterminate shoot apical meristem transformed in carpels. The flower inhibits with AP1 the formation of lateral branches and the transition from petals into stamens, the flower supports with the help of AG the

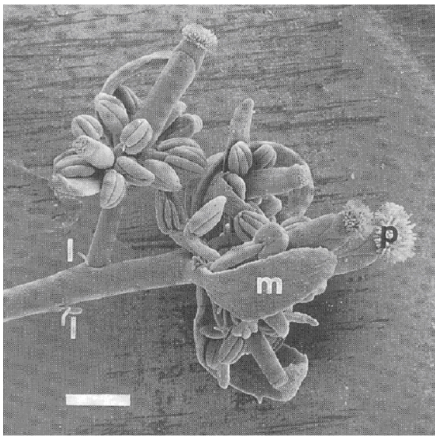

Figure 12. ap1-1 strong mutant flower. The first-whorl organs of strong mutant allele plants are bract-like, those of intermediate mutant allele plants are leaf-like, and those of weak mutant allele plants are mosaic sepaloid organs. Bowman at al. 1994

development of stamens and carpels, the organs for reproductive propagation. In the first and the second whorl is vegetative propagation suppressed, in the third and fourth whorl is vegetative propagation transformed in sexual propagation.

We have to modify the conclusion of Weigel and Meyerowitz (1994) when they wrote: “Goethe had proposed that floral organs represent modified leaves, suggesting that a vegetative leaf is the ground state of the floral organs. This has been confirmed by double and triple mutants. … In triple mutants that lack A, B, and C activities, all floral organs resemble leaves.” *The ground state of the floral organ is a vegetative leaf with its accompanying axillary bud.*

A remarkable result of molecular analysis of flowering development is that it shows a very close relationship between petals and stamens. The plant develops a ‘Janus-faced’ organ. It can ‘look’ to the periphery and shows its petal face, it can ‘look’ to the centre and shows its stamen face. Left alone in the AP2 and AG double mutants it cannot decide in which way to look, petaloid-stamens or staminoid-petals arise.

The separation of the sexes and organic disunion

“From the very beginning we have to consider this ideal body as simple as possible, and to look at it as disunited, for without the process of disuniting of an entity, a third one cannot develop.” (Goethe, 1964)

The process of organic disunion induces in embryogenesis the development of the each other complementary organised and polar orientated and situated shoot and root. The process of organic disunion in the flower has not a single starting point, but induces in two separated places by meiosis the development of the complementary organised pollen grains and embryo sacs. The stamen whorl shows in its morphology the mutual interference of the pollen grain inducing processes with the developmental process of a vegetative phytomer and the carpel whorl shows in its morphology the mutual interference of the embryo sac inducing processes with the developmental processes of a vegetative phytomer.

The mutant phenotype of PHABULOSA (phb-1d) (Mc. Conell and Barton 1998) is a good example for the close relationship of the shoot apical meristem with axillary meristems and ovules and of the leaf with the carpel. Phb-1d is a dominant mutation that causes altered leaf polarity such that adaxial characters develop in place of abaxial leaf characters. A striking feature of phb-1d mutants is that axillary meristems, normally found only adaxial in the leaf axil, develop around the entire circumference at the base of the adaxialized leaves, suggesting that their formation is correlated with adaxial cell fate (Siegfried, et al. 1999). The ovules, which normally originate from the interior (adaxial side) of the carpel, develop ectopically in the phb-1d mutant on the outside at the base of the carpel (Figure 13). The sepals are like the leaves changed in filament or trumpet like structures, and the petals are filamentous, the epidermal cells are of the adaxial type. The phenotype of the stamens is in the phb-1d mutant less changed as the phenotype of the carpel the adaxial and abaxial parts are equally developed, the aperture of the pollen sacs is moved from the adaxial to the lateral side (Mc. Conell and Barton 1998). The leafy nature of the floral organs becomes clearly visible in the phabulosa mutant phenotypes. But it is also clear, that great differences exist between stamens and carpels, the carpels show a closer relationship to the leaf and the axillary buds as the stamens.

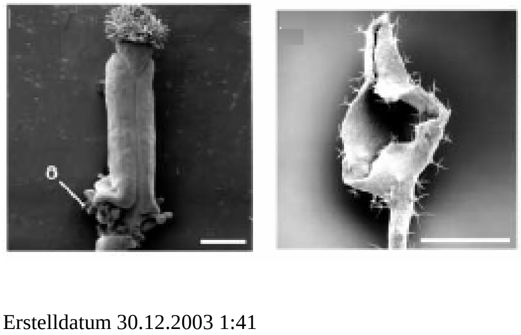

Figure 13. Phabulosa mutants. Left: *phb-1d*/+ mutant carpel showing ectopic ovules developing from the base. Right: Trumpet-shaped leaf from an individual heterozygous for the *phb-1d* mutation. (Conell and Barton, 1998).

Goethe often compared the development of seeds with the development of buds and the forces which underlie the formation of the carpels with the forces which underlie by ferns the formation of the spore bearing leaves. When we now consequently continue Goethe's point of view, we have to ask us, what are the relationships between the stamens and the vegetative plant?

We find characteristics for the root pole again as characteristics for the stamens. As far as I know there has been found at least one gene, called TIP1, which is both expressed in the root as in the flower (Schiefelbein et al. 1994). The root hairs, which arise at the apical end of the root hair cells, can be hampered in their growth after a mutation in the TIP1 gene, those impeded root hairs are shorter and occasionally branched off at their basis. The same mutation hampers the growth of the pollen tube. It is known, that both for the determination of the growth direction of pollen tubes as for root hairs there is an intracellular gradient of Calcium ions necessary (Ridge 1995). The current used terms "germination" of pollen grains, and "germination tube" point at characteristics, those has the root pole in common with the male pole of the flower.

The root organ is discerned from the leaf by continuous formation and disintegration, by the permanent conic-cylindrical shape, the absence of chlorophyll, and by the each other following processes of arise and decay of the different tissues (columella, rhizoderm, at last rests only the hypoderm which constitutes the border of the root to the surrounding earth). The lateral organs of the roots arise endogenously, inside the central cylinder; the lateral organs of the shoots arise exogenously. Petals and stamens are exposed to the light and air, but the surfaces lack stomata and chlorophyll is missing. The stamen is discerned from the carpel by his short lifetime, pollen grains arise surrounded by stamen tissue (endogenously), and ovules arise on the adaxial site of the carpel (exogenously). The plant releases the pollen grains by tearing up the pollen sacs.

Homeosis is not metamorphosis

Bateson (1894) has introduced the idea of homeosis and defined as: "the assumption by one member of a meristic series, of the form or character proper to other members of the series ..." Homeosis has not the same meaning as metamorphosis. Molecular biologists are interested in the genetic processes which occur during plant development. The induced and genetically fixed homeotic transformations are ideal research subjects.

Metamorphosis deals with the relationships between organs, how the organs are related to each other. The study of abnormal or irregular metamorphosis was for Goethe a way to find the rules for normal metamorphosis. Goethe knew only a few examples of abnormal metamorphosis compared with the wealth of abnormal forms we know today. Filled flowers and the perfoliated flowers of the rose and the carnation are mentioned in his publication (1790)[3]. The gradual transitions of one form in another can show clear relationships, like the well known transition of tepals in stamens in the Nymphea flower. Such gradual transitional stages are found only between petals and stamens in the case of Arabidopsis. The many mosaic forms we know today are only to a limited extent helpful to study the relationships between the organs. There are a lot of forms, for example mosaics of sepals and petals, mosaic forms of carpels and sepals, of foliage leaves and petals and of stamens and carpels (Bowman 1994), that conceal in spite of reveal. Mosaics arise as soon as organ primordial tissues are not separated well, independently of the nature of the primordial tissues. Almost everything goes.

It is important to discern between homeosis and metamorphosis. Both concepts are needed. I have argued here, that metamorphosis is not only a linear process of changing forms and that

---

[3] The perfoliated flowers of the rose and of the carnation may be examples of the accidental metamorphosis caused by other organisms like insects, viruses etc. and not of the irregular metamorphosis or retrogressive metamorphosis (1790 §7-8).

Goethe’s organic disunion is another form of plant metamorphosis. Another point is that we have to look at the phytomer as the unit of the plant which is transformed and not the single leaf.

Summary

Results of molecular genetics not only confirm the hypothesis of Goethe, of the leafy nature of the floral organs, they also show that the ground state of the carpel is the vegetative leaf with its accompanying bud(s). The stamen has not the same ground state as the carpel; here we find characteristics of the leaf and the root. Results of molecular genetics further confirm Goethe’s (overseen) concept of organic disunion, which leads to a new concept of the body plan of angiosperms. The first step in metamorphosis is the process of organic disunion, which leads to the polarised embryo with its shoot and root pole. The second step differentiates the shoot pole in leaf and shoot axis and the root pole in root organ and root axis. Organic disunion happens a second time in the process of the separation of the sexes. Vegetative propagation is changed in generative propagation.

Peer Schilperoord
Biologe
Hauptstrasse 16
7492 Alvaneu Dorf
Schilperoord@bluewin.ch

Literature.

Alvarez, J. and Smyth, D. R. (1999). CRABS CLAW and SPATULA, two Arabidopsis genes that control carpel development in parallel with AGAMOUS. Development 126, 2377-2386.

Arber, A., translator (1946). The metamorphosis of plants. Chronica Bot. 10, 63-126.

Bateson, W. (1894): Materials for the study of variation. Cambridge, Cambridge University press.

Berleth, T. and Jürgens, G. (1993). The role of the monopteros gene in organising the basal body region of the Arabidopsis embryo. Development 118, 575-587.

Bowman, J.L., Smyth, D.R., and Meyerowitz, E.M. (1991). Genetic interactions among floral homeotic genes of Arabidopsis. Development 112, 1-20.

Bowman, J.L., editor (1994). Arabidopsis - An atlas of morphology and development. Springer, New York.

Coen, E.S., (2001). Goethe and the ABC model of flower development. C.R. Acad. Sci. 324, 1-8.

Coen, E.S. and Carpenter, R., (1993). The metamorphosis of flowers. The Plant Cell, Vol. 5, 1175-1181.

Goethe, J.W., (1790). Versuch die Metamorphose der Pflanzen zu erklären. Gotha: Ettinger.

Goethe, J.W. (1964). edited by Kuhn, D. Goethe die Schriften zur Naturwissenschaft. Zehnter Band: Aufsätze, Fragmente, Studien zur Morphologie. Leopoldina Ausgabe, Hermann Böhlaus Nachfolger, Weimar.

Goethe, J.W. (1975). Schriften zur Botanik und Wissenschaftslehre. München, DTV Gesamtausgabe 39.

Goethe, J.W. (1977). edited by Kuhn, D.: Goethe die Schriften zur Naturwissenschaft. Neunter Band Teil A, Zur Morphologie. Hermann Böhlaus Nachfolger, Weimar.

Goto, K., Kyozuka, J., Bowman, J.L. (2001). Turning floral organs into leaves, leaves into floral organs. Current opinion in Genetics & Development 11, 449-456.

Honma, T. and Goto, K. (2001). Complexes of MADS-box proteins are sufficient to convert leaves into floral organs. Nature 409, 525-529.

Irish, V.F. and Sussex, I.M., (1990). Function of the apetala-1 gene during Arabidopsis floral development. The plant cell 2, 741-753.

Jürgens G., (1994): Pattern formation in the embryo. In: Meyerowitz E.M, Somerville C.E. (eds.): Arabidopsis. Cold Spring Harbor Laboratory Press, 297-312.

Kaplan, D.R. and Cooke, T.J. (1997). Fundamental concepts in the embryogenesis of Dicotyledons: a morphological interpretation of embryo mutants. The Plant Cell 9, 1903-1919.

Long, J.A. and Barton, M.K., (1998). The development of apical embryonic pattern in Arabidopsis. Development 125, 3027-3035.

Long, J.A., Woody, S., Poethig, S., Meyerowitz, E. M., Barton, M. K., 2002. Transformation of shoots into roots in Arabidopsis embryos mutant at the TOPLESS locus. Development 129, 2297-2306.

Mayer, U., Torres Ruiz, R.A., Berleth, T., Miséra, S. and Jürgens, G. (1991). Nature 353, 402-407.

Mayer, U., Büttner, G. and Jürgens, G. (1993). Apical-basal pattern formation in the Arabidopsis embryo: studies on the role of the gnom gene. Development 117, 149-162.

Mc. Connell, J.R. and Barton, M.K. (1998). Leaf polarity and meristem formation in Arabidopsis. Development 125, 2935-2942.

Pelaz, S., Tapia-López, R., Alvarez-Buylla, E.R., Yanofsky, M.F. (2001). Conversion of leaves into petals in Arabidopsis. Current Biology 11, 182-184.

Pruitt, R.E., Bowman, J.L., and Grossniklaus, U. (2003). Plant genetics: a decade of integration. Nature genetics supplement 33, 294-304.

Ridge R.W. (1995): Recent development in the cell and molecular biology of root hairs. Journal of Plant Research; 108, S. 399-405.

Scheres, B., Wolkenfelt, H., Willemsen, V., Terlouw, M., Lawson, E., Dean, C. and Weisbeek, P. (1994). Embryonic origin of the Arabidopsis primary root and root meristem initials. Development 120, 2475-2487.

Schiefelbein J.W., Benfey P.N., (1994): Root development in Arabidopsis. In: Meyerowitz E.M, Somerville C.E. (eds.): Arabidopsis. Cold Spring Harbor Laboratory Press; S. 335-353.

Schilperoord-Jarke, P.C. (1997). The concept of morphological polarity and its implication on the concept of the essential organs and on the concept of the organisation type of the dicotyledonous plant. Acta Biotheoretica, S. 51-63.

Schilperoord-Jarke, P.C. (2000). Goethes Metamorphose der Pflanzen und die moderne Pflanzengenetik. In: Heusser, P., editor (2000). Goethes Beitrag zur Erneuerung der Naturwissenschaften. Paul Haupt Verlag, Bern, p. 131-171.

Siegfried, K.R., Eshed, Y., Baum, S.F., Otsuga, D., Drews, G.N. and Bowman, J.L., (1999). Members of the YABBY gene family specify abaxial cell fat in Arabidopsis. Development 126, 4117-4128.

Sitte, P., (1991): Morphologie und Anatomie der Sprosspflanzen. In: Sitte P., Ziegler H., Ehrendorfer F., Bresinsky A.: Lehrbruch der Botanik für Hochschulen. Gustav Fischer Verlag Stuttgart; S. 170.

Talbert, P.B., Adler, H.T., Parks, D.W. and Comai, L., (1995). The REVOLUTA gene is necessary for apical meristem development and for limiting cell divisions in the leaves and stems of Arabidopsis thaliana. Development 121, 2723-2735.

Theissen, G., Saedler, H. (2001). Floral quartets. Nature 409, 469-471.

Theißen, G. (2001). Development of floral organ identity: stories from the MADS house. Curr. Opin. Plant Biol. 4, 75-85.

Torres-Ruiz, R.A., Lohner, A. and Jürgens, G. (1996). The GURKE gene is required for normal organization of the apical region in the Arabidopsis embryo. The Plant Journal 10(6), 1005-1016.

Troll, W., 1926. Goethes morphologische Schriften. Eugen Diederichs - Verlag, Jena.

Troll, W., (1967). Vergleichende Morphologie der höheren Pflanze. Teil 1. Nachdruck. Königstein/T, Otto Koeltz.

Waites, R. and Hudson, A. (1995). Phantastica: a gene required for dosiventrality of leaves in Antirrhinum majus. Development 121, 2143-2154.

Weigel, D., Meyerowitz, E.M. (1994). The ABCs of floral homeotic genes –Review. Cell., Vol. 78, S. 203-209.

White, J., (1984). Plant Metamerism. In: Dirzo R., Sarukhan J. (eds.) Perspectives on plant population biology. Sunderland Sinauer; S. 15-47.