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'Underground plant mobility' and 'dispersal of diaspores.' Two exemplary case studies for useful examinations of functional morphology (plant construction)

Norbert Pütz & Karl H.A. Schmidt

Botanisches Institut, Spezielle Botanik, R.W.T.H. Aachen, D - 52056 Aachen, Germany

Abstract. *– Two exemplary case studies of functional morphology are presented. The first topic, underground plant mobility, illustrates the feedback effect of 'plant structure' and observation of their 'functional role'. Questions are raised in relation to both, 'plant structure' and its 'functional role'. Experiments are developed to obtain answers, and to prompt further questions resulting from these answers. This was shown in an exemplary way in the unusually geophilous strategies of* Hemerocallis fulva, *well adapted to fulfilling the function 'cryptical survival'. Thus, investigation of functional morphology is useful for a better understanding of plant behaviour. The second case study relates to dispersal of diaspores in Apiaceae. Wind tunnel experiments were carried out to analyze the 'flying ability' of winged or spiny mericarps. In general, winged diaspores fly better than spiny ones, except in the case of* Daucus muricatus, *the spiny diaspores of which fly better than the winged ones, e.g., of* Prangos pabularia. *Thus, this topic was useful in showing that functional approaches to 'plant structure' may reveal new perspectives in ecological understanding. However, 'form' and 'function' are frequent in botanical literature, showing that a dualistic treatment of plant structures is very helpful for a better understanding of plant biology. Besides 'underground plant movement' and 'dispersal' there are important topics such as 'floral ecology', 'biomechanics', and many more. All of these could be included in one category, which we propose to call 'plant construction'. Scientific work on 'plant construction' should be based on three basic principles: 1. The starting point of the investigation should be the specific form itself, 2. The scientific question should be functional, and 3. Scientific investigation should be based on targeted observation and experiment.*

Key words. *– Plant construction, contractile root, shoot elongation, dispersal, experiment, functional morphology,* Hemerocallis fulva.

Introduction

It is useful at the outset to give a short definition of the meaning of 'morphology'. In general, 'morphology' is 'the study of plant organs from the standpoint of their form relation' (Arber 1925). However, as Riedl (1983) describes, especially in the United States 'morphology' is often viewed "as obsolete, almost as a 'dirty word', which one would never dare to use in a grant proposal. It would be better to speak of 'structural design' or 'pattern of features' if one wanted one's grant approved." (Riedl 1983: 206).

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This unfavorable point of view could be said to be not only highly ignorant, but to forget the important role of 'morphology' for botanical understanding. The traditional methodological approach to plant forms is 'comparison'. "Morphology contains the methodology of scientific comparison, namely, the distinction between essential similarities (homologies) and accidental similarities (analogies)." (Riedl 1983: 206).

'Comparative morphology' has played and will play an important role in discovering typical patterns in plant forms ('plant structure', 'plant design', 'Gestalt', 'Bau'). We know a large quantity of traditional work of great quality, e.g., the research in plant development by W. Hofmeister (see Kaplan & Cooke 1996), *Die Blüthendiagramme* by Eichler (1875) and many more. Thus, plant structures ('anatomy' and 'morphology') are the basis of botanical training, however, their innovation potential for modern analysis in botany is thought to be small, and thus 'morphology' is currently disfavored.

However, Kaplan & Groff (1995) emphasize not only evolutionary but also functional significance: "Any attempt to evaluate the structural evolution of organisms must do so from two complementary perspectives: the organizational theme or Bauplan characteristic for the group and the functional or adaptive features of its structure." According to Weber (1958) or Froebe (1985), these two aspects could be termed 'organization' and 'construction'. "Organization refers to the morphological relationships of structure, reflecting the evolutionary history of the group, whereas construction refers to the functional role of these structural features." (Kaplan & Groff 1995: 111).

In this paper, we would like to give two examples of experimental work which deal with 'plant form' and its 'functional role' for the individual plant. Based on these two case studies, we will try to suggest principles for work on 'plant construction'. This is a manuscript version of an oral presentation held at the 13. Symposium Morphology, Anatomy and Systematics in Leuven (Pütz 1996d).

Table 1. Selection of taxa having root contraction.
Listing of single taxa is exemplary, showing that root contraction is widespread in higher plants.

Pteridophyta: Ophioglossaceae (*Ophioglossum multifidum*, Stevenson 1975)

Spermatophyta - Cycadophytina: Cycadaceae (*Cycas revoluta*, Watenabe 1925; *Zamia* spec., Stevenson 1980)

Spermatophyta - Magnoliophytina - Magnoliatae (Dicotyledonae):

Apiaceae (*Carum carvi*, deVries 1880), Asteraceae (*Cichorium intybus*, Rimbach 1929), Boraginaceae (*Symphytum officinale*, Rimbach 1929), Brassicaceae (*Brassica napus*, deVries 1880), Caryophyllaceae (*Saponaria officinalis*, Rimbach 1929), Cucurbitaceae (*Bryonia alba*, Rimbach 1929), Fabaceae (*Melilotus album*, Bottum 1941), Lamiaceae (*Salvia pratensis*, Rimbach 1929), Moraceae (*Ficus benjamina*, Zimmermann et al. 1968), Polygonaceae (*Rumex acetosa*, Rimbach 1929), Ranunculaceae (*Ranunculus bulbosus*, Rimbach 1897), Rosaceae (*Bromus* spec., Molisch 1965), Scrophulariaceae (*Verbascum thapsus*, Rimbach 1929), Solanaceae (*Atropa belladonna*, Rimbach 1896)

Spermatophyta - Magnoliophytina - Liliatae (Monocotyledonae):

Agavaceae (*Agave americana*, Rimbach 1922), Alliaceae (*Allium sativum*, Rimbach 1929), Amaryllidaceae (*Narcissus pseudonarcissus*, Draheim 1922), Araceae (*Philodendron bipinnatifidum*, Rimbach 1922), Arecaceae (*Phoenix canariensis*, Rimbach 1922), Asparagaceae (*Asparagus officinalis*, Rimbach 1927), Convallariaceae (*Polygonatum multiflorum*, Stroever 1892), Hyacinthaceae (*Muscari comosum*, Kirchner et al. 1934), Iridaceae (*Gladiolus segetum*, Galil 1969), Lilaceae (*Lilium martagon*, Rimbach 1927), Musaceae (*Musa ensete*, Rimbach 1922), Orchidaceae (*Cattleya crispa*, Stroever 1892)

Case study 1. Underground plant mobility

Many species possess contractile roots (see table 1), the visible features of which are firstly, swelling of the proximal parts, and secondly, shrinkage of the root surface.

The functional role of contractile roots is assumed to be soil depth regulation (e.g., de Vries 1877, 1880; Stroever 1892; Rimbach 1898; Arber 1925). Thus, the study of contractile roots is very interesting in relation to mechanism, causality of external factors, and ecological necessity. There are several different approaches to the anatomical mechanism, and a re-evaluation of the different hypotheses is given in Pütz & Froebe (1995).

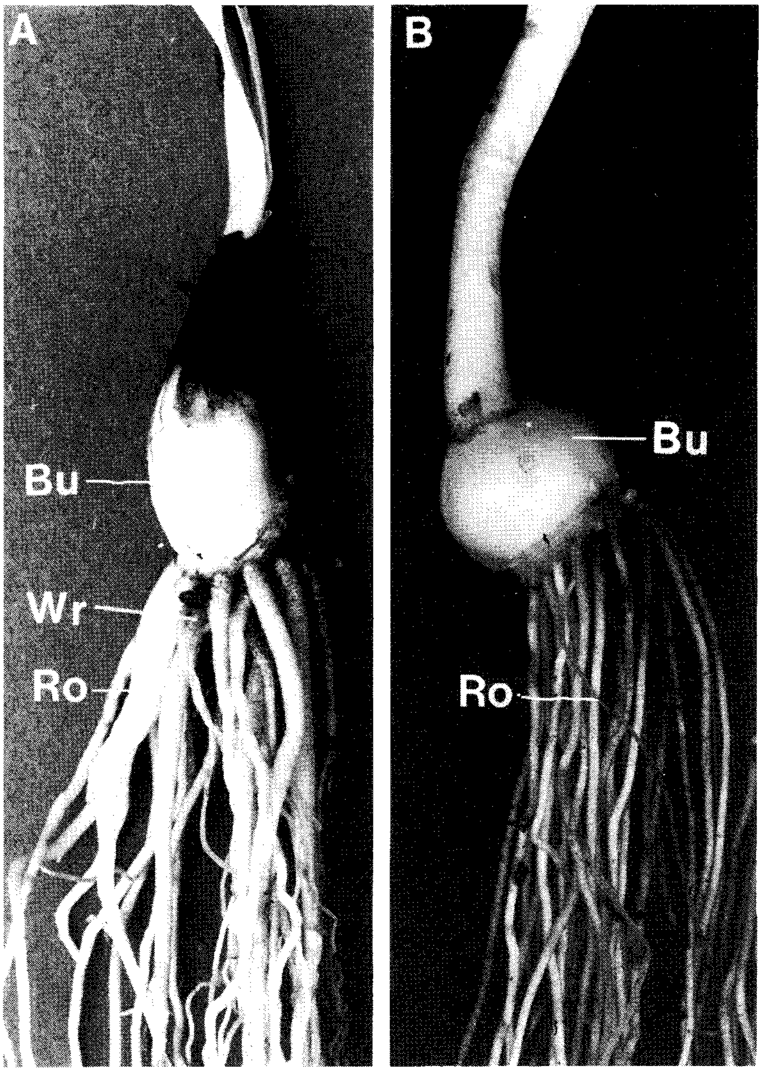

Figure 1. Bulbs of Nothoscordum inodorum *planted shallowly (A) or at a depth of 20 cm (B). The deeply planted bulbs are globular and have small roots, while the shallow bulbs are egg-shaped, of smaller diameter and produce larger, wrinkled roots. Bu, bulb; Ro, Roots; Wr, wrinkling of the surface.*

However, the causal-analytical approach did not exist, and in recent years we have done many experiments on contractile roots and their importance for plants. We do not wish to go into great detail in this paper but, to show the feedback effect of 'plant form' and experiments, questions are raised concerning 'plant form' and its function, and experiments are developed to obtain answers, and to prompt further questions resulting from these answers.

The development of 'time lapse photography' made it possible to observe underground movement directly. In several studies, we have shown photo-series of different species and the moving processes during the vegetation period. In some cases, the moving body is the cryptocorm (e.g., a corm, a bulb, a ramet), and movement occurs by the activity of the moving organ, the contractile root (e.g., Rimbach 1898, Pütz 1993, 1996b). In others, underground movement is due to axis growth of the rhizome (e.g., Arber 1925, Mohr & Schopfer 1995, Raunkiaer, 1934). Sometimes, movement is effected by both, root contraction, and axis growth (Pütz 1994, 1996a). A final principle of movement is realized in many turnips, by root and stem contraction (e.g., Stevenson 1980, Pütz & Sukkau 1995). In general, we found that movement was favorable for the plants in several respects, (a) securing a safe position in the soil; (b) vegetative spreading of daughter bulbs or corms; and (c) achieving an ecologically useful position (see Pütz 1996c).

Movement occurs underground, and the question is raised as to how plants are able to move against soil resistance. Using various biomechanical approaches, we quantified not only pulling force using the lifting technique (Pütz 1992), but also discovered and quantified the soil channel building as another important activity of contractile roots in supporting underground movement (Pütz et al. 1995).

The next question leads on to the causality of contractile root development. Does planting depth influence the formation of contractile roots? Or, seen from the standpoint of the plants: does a plant detect its depth, and show a specific reaction? Rimbach (1897) and Halevy (1986) did some initial work, and we have made further observations and found great differences in the development of contractile roots in some species. In pot culture experiments we found, that *Nothoscordum inodorum* (Ait.) Nichols. develops thick wrinkled contractile roots only when the sheath leaves are illuminated during sprouting. If the first 20 cm of the sheath leaves are darkened during sprouting, the roots remain smooth and small (fig. 1; see also Pütz 1996b).

Table 2.
Features of single contractile roots of *Sauromatum guttatum* grown under various conditions.
L+: light induction, L-: without light induction. t+: temperature induction in the previous vegetation period, t-: no temperature induction (for further details see Pütz 1997).
n = average of measured roots, AW = average work and standard deviation, RT = average root thickness, SU = surface.

parameter	n	AW [J]	RT [mm]	SU
L+	87	0.36 ± 0.08	5.4 ± 1.2	wrinkled
L-; t +	43	0.13 ± 0.03	5.2 ± 1.1	wrinkled
L-; t-	43	0.00 ± 0.00	3.6 ± 0.8	± smooth

In some species, the experimental set necessarily involves more work. In *Sauromatum guttatum* we found similar form changes, but in pot experiments we were unable to discover the parameters responsible. In a biomechanical approach, we measured the physical component of single contractile roots, the force (in Newtons), and the work (in Joules) to identify root activity. Plants were grown in a mist culture system, and root activity was measured using the lifting technique (Pütz 1992). We succeeded in inducing root activity by light illumination on the sheath leaves during sprouting. Also, a significantly smaller contraction activity was induced by day-night temperature changes in the previous vegetation period (Pütz 1997). However, in both cases the root shape was very similar (see table 2). Differentiation was not linked to morphological characteristics but related to physical data of root force, and, of course, the function of pulling the cryptocorm deeper. Only when both triggering mechanism are not present, i.e. no light and no temperature induction, roots remained smaller (but not significantly smaller than the active roots, see table 2), and had no contractile activity.

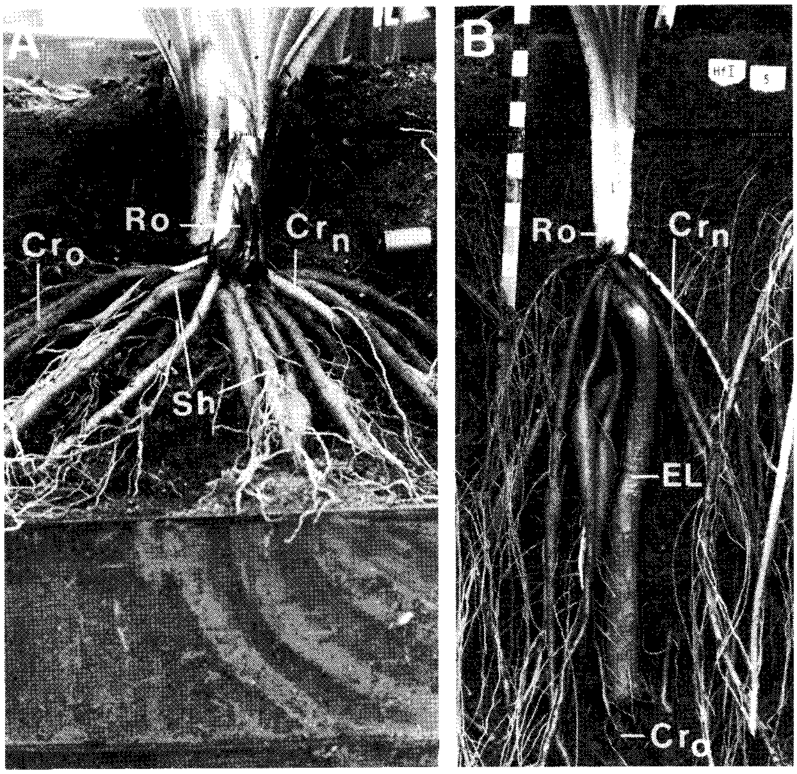

Figure 2. Shallowly planted individuals of Hemerocallis fulva *(A) form a rosette of leaves at the top of the short vertical stem and a circle of new roots just above the old roots. Individuals planted at a depth of 25 cm (B) elongate their shoot during sprouting. A rosette of leaves and a circle of new roots are formed a few centimeters below the soil surface, and several centimeters away from the old position. These shoots only appear at very deep soil positions, and are thus called 'facultative shoot elongation'. EL, elongation of the axis; Ro, rosette; CR, contractile roots (o, old root tubers from the last vegetation period; n, new roots), sh, shrinkage.*

Finally, we did the same experiments with *Hemerocallis fulva* L. We found permanent root activity, even in plants which were covered up to 70 cm and were cultivated under constant temperatures (Pütz 1998). Thus, the question arises as to how individuals of *H. fulva* react on becoming too deep into the soil. In some further observations, we found a very surprising reaction. In shallow-planted individuals the new root circle appeared just above the old one (fig. 2A). The new root tubers show strong contractile activity and pull the cryptocorm downwards. Deeply planted cryptocorms of *H. fulva* (see fig. 2B) move upwards by the growing activity of the shoot tip. During the sprouting process, a few internodes of the deeply-located shoot tip elongate up to 10 - 25 cm, and the new root circle and the leaf rosette appear at the top of this new axis, only a few centimeters below the soil surface. In contrast to many rhizomatous plants, which show a regular interval between shortened and elongated rhizome-parts, elongation in *Hemerocallis* only occurs when the individual is positioned very deeply in the soil. We call this reaction 'facultative shoot elongation'. The geophilous strategies of *Hemerocallis fulva* are unusual, however, they are well adapted to fulfill the function of 'cryptical survival'.

However, this throws up further questions. For example, how does the plant detect its deep position? Darkening the basal leaves during sprouting using PVC tubes had no effect in *Hemerocallis* on shoot elongation. The parameters involved in the extensive shoot elongation are unknown and future experiments will deal with this topic.

Comment to case study 1

According to Goebel (1908) it is the role of 'experimental morphology' to ask why a given development takes place. "Wenn also die Entwicklung abgeändert werden kann, so fragt es sich naturgemäß, wodurch dies erfolgt. Die Antwort kann nur dadurch gegeben werden, daß wir die Entwicklung zu beeinflussen suchen, indem wir die Bedingungen, unter denen sie sich vollzieht, abändern. Dies geschieht auf dem Wege des Experiments. Die Entwicklungsgeschichte ist demgemäß fortgeschritten von einer beschreibenden zu einer experimentellen." (Goebel, 1908: 2; translation: If development is modifiable, the question arises as to how this happens. We can only find the answer by attempting to modify development by changing the conditions under which development normally occurs. This is done experimentally. Thus, plant development evolves from the descriptional to the experimental).

In contrast to this, Troll (1937) sees the role of experiments in 'morphology' to show 'form changes' for a better understanding of morphological types: "In Anbetracht solcher oder ähnlicher Erscheinungen kann man als die morphologische Aufgabe der experimentellen Methode die Feststellung der unter bestimmten Außen- und Innenbedingungen möglichen Formveränderungen der Pflanze bezeichnen." (Troll 1937: 42; translation: In considering these or similar phenomena, we can define the morphological task of experimental sets as to find out the potential form modifications of plants under defined inner and outer conditions). He rejects the experimental approach of Goebel, because it would lead to 'developmental physiology': "Bei rein kausaler Behandlung geht die experimentelle Morphologie über in die Entwicklungsphysiologie" (Troll 1937: 39; ranslation: If treated on a purely causal level, experimental morphology merges into the physiology of development).

Observing, for example the 'facultative shoot elongation' of *Hemerocallis fulva,* our experiments show the capability of an organ to build up different kinds of structural features according to Troll (1937). Furthermore, our experiments show the dependence on external conditions according to Goebel (1908). Thus, our experiments relate to both 'morphology' and 'physiology' and can show the continuum between both divisions.

In relation to the unexpected form-change of *Hemerocallis fulva,* a further aspect presents itself. Looking at the plant as a whole, we have to ask: which function has this form-change? Our experiments thus become of great ecological importance. The form and its change related to external factors is seen against the background of its ecological function. The 'facultative shoot elongation' of *Hemerocallis fulva* functions as an emergency response to unfavorable conditions (Pütz 1998), in order to increase the chance of plant survival in the habitat ('cryptical survival').

The 'plant form' or 'structural design' is of fundamental interest in relation to different biological divisions, if its adaptation to a specific function is taken into account. From this point, scientific analysis becomes dualistic, i.e. an approach to both 'form' and 'function'. This is appropriate, especially in topics such as 'underground plant mobility'. The significance of results from this dualistic approach is biological, currently called ecological. Moreover, it might be argued that in topics such as 'underground plant mobility', a one-sided investigation is of no utility.

Case study 2. Dispersal of diaspores in some Apiaceae

It is appropriate to present another topic, quite different from case study 1. Dispersal of diaspores is an ecological topic of great interest, because it deals with distribution of species, as well as the acquisition of space for development (compare van der Pijl 1972; Müller-Schneider 1983). Experiments in this field are useful in several respects, one of these being to test the hypothesis suggested by looking at the 'structural design'. We completed extensive wind tunnel experiments (compare Clegg & Grace 1974; Ehrendorfer et al. 1980) to analyze the 'flying ability' of mericarps in several species of the Apiaceae (Schmidt 1991, Schmidt & Pütz, in prep.). In the context of this paper, we would like to present only a fraction of these experiments.

Table 3. Wind tunnel experiments: measurement of average drift of some mericarps of Apiaceae.
See Schmidt & Pütz in prep.; technical data: wind velocity 2 m/s [Beaufort 2 = light wind, 'leichte Brise'], laminar streaming, height of fall 58.5 cm.

species		drift (cm)	weight (g)
Prangos pabularia	winged	15 ± 2	0.0500
Thapsia garganica	winged	75 ± 9	0.0313
Artedia squamata	winged	63 ± 9	0.0131
Orlaya daucoides	spiny	13 ± 2	0.0376
Daucus muricatus	spiny	30 ± 4	0.0150

Mericarps of species, such as *Thapsia garganica* L., *Prangos pabularia* Lindl. or *Artedia squamata* L. have wings which are easy to observe. Others, such as *Orlaya daucoides* (L.) Greuter or *Daucus muricatus* (L.) L., are spiny (see fig. 3). A functional interpretation on the basis of the 'structural design' leads us to expect that the winged mericarps are well-adapted to wind dispersal, whereas the spiny ones are well-adapted to epizoochory. We completed our experiments to obtain quantitative data about dispersal, and to check the hypotheses about the function of the 'structural design'. We tested flying ability and average drift under constant wind conditions. Our results (table 3) gave a quantitative basis for stating that winged diaspores of *Thapsia garganica* and *Artedia squamata* are well adapted to flight. On the other hand, the spiny *Orlaya daucoides* diaspore flew very badly. Finally, it was most surprising to us that our results showed that the spiny diaspore of *Daucus muricatus* is a better flyer than the winged diaspore of *Prangos pabularia*. Considering the weight of the diaspores (table 3), one can assume that the good flying behavior of *Daucus* is achieved by its lighter weight. Our results, once again, lead us to further questions. What happens under natural conditions? How great is the maximum range of dispersal in the species examined?

Comment to case study 2

The dispersal of Apiaceae is an interesting and ecologically important topic, and we are going to discuss it in another paper (Schmidt & Pütz, in prep.). However, we have chosen this example here because it demonstrates that experiments with plant structures reveal new perspectives in understanding the function of a specific 'structural design'. Our results (table 3) make clear that the interpretation of 'fitness to fly' does not depend only on characteristic structural features (e.g. wings) of the diaspore, but involves many parameters, defined by the physical science of flight, e.g. weight, value of cw (drag coefficient), transverse plane or quality of diaspores surface (compare e.g., Hertel 1963). Furthermore, we have to include biological parameters, such as height of plant or 'take off strategy' of anemochorous diaspores', on which we are focusing our experiments at the moment.

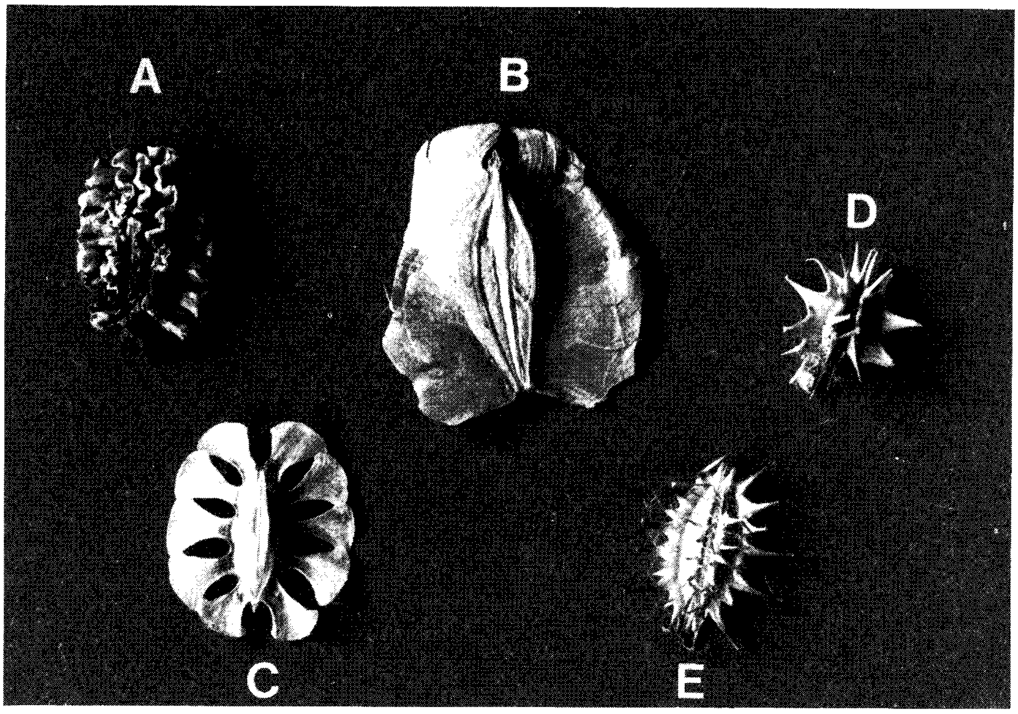

Figure 3. Mericarps of (A) Prangos pabularia, *(B)* Thapsia garganica, *(C)* Artedia squamata, *(D)* Orlaya daucoides *and (E)* Daucus muricatus.

However, in general, our experiments make clear that we understand important ecological topics better if quantitative data from experiments are obtainable. Experiments provide a real base for functional interpretation, i.e. which structural adaptations are most important in fulfilling a defined ecological function in the best possible way. On the basis of experimental data we are able to discuss syn-ecological interplay in plant formations (ecosystems), not only in a general way, but also with special regard to the possibilities of any single individual.

Conclusions

Our case studies have shown that (1) a dualistic approach to 'form' and 'function' is often most appropriate, and that (2) experimental analysis can give functional interpretations a quantitative basis.

Currently, there exist many important investigations to confirm these two statements. In addition to topics such as 'underground plant mobility' and 'plant dispersal', we would like to mention two investigations which are exemplary.

'Floral ecology' (Blütenbiologie). This biological topic is based on Sprengel (1793). It has a long tradition and is well established. Kugler (1970) distinguished between several periods, the first based on accurate observation, the last based on experiment: "So kommen wir zur dritten Periode, der experimentellen Blütenbiologie. Sie wurde von zoologischer Seite durch die klassischen Untersuchungen v.Fritschs mit der Honigbiene und von botanischer durch die exakten Besuchsanalysen Knolls (1926) eingeleitet" (Kugler 1970: 3; translation: Thus, we come to the third period, experimental floral ecology, which from a zoological standpoint was initiated by the classical examination of v. Fritsch, and, botanically, by the exact visitor analysis of Knoll).

'Plant biomechanics' is based on various fundamental works, e.g., Schwendener (1874) or Rasdorsky (1928, 1930). Niklas (1992) defined the aim of plant biomechanics (actually the aim of his textbook called *Plant biomechanics*) "... to explore how plants function, grow, reproduce, and evolve within the limits set by their physical environment." Experiments carried out in 'plant biomechanics' are of great biological interest and deal with many topics, including for example: "biomechanics and multicellularity in plants" (Niklas & Kaplan 1991); "bending stability" (Speck et al. 1990, Spatz & Speck 1995); "tree design" (Mattheck 1992), "anchorage systems" (Ennos et al. 1993); "aerodynamic behaviour of diaspores" (Green 1980, Mayer 1995). It is important to note that biomechanics in several cases has an 'applicability' (e.g., Mattheck 1992) and shows a strong connection to the engineering biology called 'bionics' ('Bionik', Nachtigall 1992).

All of these important investigations are difficult to integrate into a defined traditional dimension. We firmly believe that all of these topics would best be grouped in one category. This category could be called 'functional', 'experimental', 'causal' or 'biomechanical', and always have a strong connection to 'structural design'. All of these attributes seem to be included in 'functional morphology'. Speck (1997) proposed grouping these topics in 'eco-biomechanics'. However, we firmly believe that it is most useful to give this category a different name from existing ones such as 'morphology', 'biomechanics' or 'ecology', and we propose calling this category „plant form and function" (Givinsh 1986), or, more precise, **'plant construction'**.

The basic principles of 'plant construction' should be:
1. The specific 'structural design' itself should be the starting point of the investigation.
2. The scientific question should be functional or causal: what are the reasons for a given structure?
3. Targeted observation and experiment should be the basis of investigation.

Outlook

In the 19th century, G. Haberlandt focused on causal and ecological principles in 'plant anatomy'. His *Physiologische Pflanzenanatomie* (Haberlandt 1884) was the first work to replace the descriptive division of plant tissues into a functional one. Up to the present 'plant anatomy' has been functional, always linked to current questions in botany.

Karl von Goebel tried to do the same at the level of 'morphology', i.e. at the level of the 'Gestalt' (compare his *Organographie der Pflanzen*, Goebel 1928-1933). He used various methods: scientific comparison, ecological observation, physiological experiment, and phylogeny to explain the plant as a whole. However, what was useful for 'plant anatomy', was too far ahead of its time for 'morphology'.

Later, 'morphologists' worked hard to obtain a fundamental knowledge of 'plant structures'. However, the functional role was only infrequently taken into account. Therefore, Goebel´s attempt was not successful.

More than fifty years later, the causal-ecological approach of Goebel is still essential in botanical science:

Why has a plant a specific 'structural design'?
From an evolutionary point of view answers to this question focus on 'adaptive evolution' (compare Niklas 1992, 1997). However, considered in the sense of understanding the biology of an individual plant (as we would like to do in the present paper) we can give useful answers in two respects:
(1) the structural design is influenced by external parameters; or
(2) the structural design has to fulfill a biological function.

Thus, all work done in this causal and ecological context could be integrated into 'plant construction' as defined above. Establishment of 'plant construction' is appropriate in focusing on dualistic investigation as an approach to form and function. 'Plant construction' creates a useful continuum from structural design ('morphology') to 'physiology' and 'ecology', and thus, creates a continuum from traditional to modern questions in botany. 'Plant construction' can provide a clear focal point for the excellent and important biological work, which is currently being carried out in the various fields of botanical science.

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