

Underground plant movement.

IV. Observance of the behaviour of some bulbs with special regard to the induction of root contraction.

NORBERT PÜTZ

R.W.T.H. Aachen, Biologie I, Abteilung Morphologie der Pflanzen, 52056 Aachen, Germany
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Summary

Shallowly planted bulbs of *Galtonia candicans* (Hyacinthaceae) and *Narcissus tazetta* (Amaryllidaceae) show underground movement. This movement results from the activity of the contractile roots which manifests itself in two macroscopic features, swelling of the proximal root parts and wrinkling of the root surface. The bulb remains vertical during this downward movement.

Plants register their position in the soil and are able to regulate the contractile activity of the roots. Our experiments with *Narcissus tazetta* and *Nothoscordum inodorum* (Alliaceae) show that temperature changes, pre-induction and gradients of chemical compounds have no effect on the activity of the contractile roots, they are influenced only by illumination of the basal parts of the leaf. When the basal parts of the leaf are screened, the bulb produces very thin roots that display no sign of contractile activity.

Key words: root contraction, contractile root, induction, *Nothoscordum*, *Narcissus*, *Galtonia*, Monocotyledons

Introduction

Many bulbs are able to move downward to reach a safe position in the soil (e.g., RIMBACH 1898, ARBER 1925, TROLL 1943). In some cases this downward movement is achieved with the help of runners (e.g., TROLL 1943, GALIL 1980). In most cases, however, movement is the result of root contraction, a phenomenon about which our knowledge is still very incomplete (PÜTZ 1996).

Five typical kinds of underground movement in Monocotyledons have been described in principle (PÜTZ 1991), and meanwhile it has been possible to observe underground movement behavior directly and to show it as time lapse photography¹⁾. We have thus demonstrated the unusual tilting-twisting movement of *Nothoscordum inodorum* bulbs (PÜTZ 1993), and the extensive vegetative spreading of *Oxalis pes-caprae*

(PÜTZ 1994). Moreover, the combined movement of axis growth and root contraction was analysed in *Sauromatum guttatum* in comparison with *Arisarum vulgare* and *Arum italicum* (PÜTZ 1996a).

However, the most typical underground movement, as vertical movement seems to be, has not been analyzed in detail to date. The reason for this is that many species react very sensitively to being dug out and an analysis of underground movement was therefore impossible (cf. *Allium ursinum*, *Hyacinthoides non-scripta*, *Narcissus pseudonarcissus*, *Lilium martagon*, *Zephyranthes candida*, *Eucomis punctata*, *Muscari comosum*, *Fritillaria meleagris*). Fortunately, we found some less sensitive species that made direct observation possible.

From a functional point of view, three aspects of underground movement are important (PÜTZ 1996a): (1) reaching a suitable soil position, (2) securing this safe position and (3) vegetative spreading of lateral buds. These are of great ecological interest, because soil conditions (e.g., temperature, water) are more stable at depth and deeply buried cryptocorms are less likely to be subjected to drying or freezing during the dormancy

¹⁾ In previous papers (PÜTZ 1993, 1994) this was designated 'quick motion pictures', however, 'time lapse photography' seems to be more appropriate.

period. However, less is known about the capacity of a plant to react to different soil depths. RIMBACH (1897) described a decrease in contractile root activity in deep planted corms of *Arum maculatum*, as do IZIRO & HORI (1983) and HALEVY (1986) for deep-planted corms of *Gladiolus*. In *Allium ursinum*, RIMBACH (1897a) found deeply positioned bulbs developing horizontal roots thus making downward movement of the bulb impossible. These examples make clear that at least some species are able to register their soil position. We therefore attempted to learn something about the parameters necessary for inducing contractile root activity.

Materials and methods

Narcissus tazetta L. (Amaryllidaceae). Bulbs collected in Paros (Greece) in 1991.

Galtonia candicans (BAK.) DECNE. (Hyacinthaceae). Bulbs from Botanischer Garten Aachen.

Nothoscordum inodorum (AIT.) NICHOLS. (Alliaceae). Bulbs from Botanischer Garten Aachen.

Ten bulbs each of *Narcissus tazetta* and *Galtonia candicans* were cultivated in special test containers in the green house at the Botanical Institute of the R.W.T.H. Aachen. In each container one bulb was planted approximately 10 mm beneath the soil surface. At regular intervals (2–4 weeks), plants were dug out carefully from one side and photographed. A detailed description of the cultivation parameters, the test containers and the preparation method can be found in PÜTZ (1993). Time lapse photography of some of the individuals was carried out. When the individuals were planted, an aluminium control mark was located a few cm away from the corm. The distance from the plant body to this control mark measured its underground movement. In the time lapse photography, the control marks appear as white control lines.

To understand the role of the various parameters on contractile activity of the root, 40 bulbs each of *Narcissus tazetta* and *Nothoscordum inodorum* were selected during their dormancy. Only plants which had grown in shallow soil positions were used. Each bulb was cultivated in a pot (Fa. Richard Sankey & Son, LTD, Nottingham, England, Vol. 10 l), filled with riddled sand/loam mixture. Half of the individuals were cultivated in a greenhouse with a minimum temperature ranging from 14 °C at night to 22 °C during the day (on hot summer days maximum temperatures were measured up to 35 °C, even in the shade). The remaining plants were cultivated in a phytotron at a constant temperature of 20 °C (± 1 °C). The plants were illuminated for 12 h daily with plant lamps (Osram, Power Star HQI-T 400 W/DH).

In both, greenhouse, and phytotron, half of the individuals were planted approximately 10 mm beneath the soil surface. Thus, during sprouting nearly all parts of the leaves were illuminated. The remaining individuals in each culture room were also planted 10 mm beneath the soil surface, but were cultivated with darkening of the basal leaf parts to simulate a deep soil position. This was achieved using dark PVC tubes (diameter 60 mm), through which the individual had to grow during sprouting. The tubes were resting on the soil surface

and were filled with small, dry beads of black foam rubber, the first 200 mm of the leaves thus being protected from any illumination. After three months the plants were completely dug out, the number of (contractile) roots, their diameter, and the size of the bulbs were recorded.

Abbreviations used in the text

T15 bulbs in the greenhouse, with day-night temperature changes from 10–20 °C.

T0 bulbs in the phytotron at constant temperature (20 °C)

L+ bulbs with light illumination on the basal leaf parts

L– bulbs without light illumination on the first 200 mm of the leaves.

Results

The bulbs of *Narcissus tazetta* and *Galtonia candicans* showed extensive underground movement. Our cultivation conditions made it possible to cultivate *Galtonia candicans* over a period of 15 months without a dormancy. The time lapse photography make clear that during this 15 months there was a continuous downward movement (Fig. 1). Bulbs increased in size, developing new contractile roots successively at the base. The bulbs remained upright, and thus movement can be described to be vertically downward (PÜTZ 1991). Downward movement of the bulb in Fig. 1 was about 60 mm (measured from bulb base to control line) and this plant showed more movement than all other *Galtonia candicans* bulbs tested. Bulb movement in the other individuals varied. One bulb also showed a large movement of 55 mm, while another six individuals reached a position 20–30 mm deeper, and two individuals showed only a few mm of downward movement.

In *Narcissus tazetta* there was a very similar movement (Fig. 2A–E). The bulb remained upright whenever movement occurred. At its base, contractile roots appeared successively creating a continuous downward pulling of the bulb. In some cases, a very slight secondary modification (PÜTZ 1993) in the relative position of older roots was visible, resulting from continuous bulb movement (arrow in Fig. 2D). In *Narcissus tazetta* all tested bulbs showed a downward movement of 20–30 mm. After the summer dormancy in the position of Fig. 2E, the individual was observed for a further vegetation period (Fig. 2F–K). Downward movement continued and the individual again reached a position 30 mm deeper during the vegetation period. The mother bulb remained of relatively constant size, but now lateral bulbs also appeared. Mother and daughter bulbs were very strongly connected, and there was no separation of daughter bulbs, as we have described for *Nothoscordum inodorum* (PÜTZ 1993). Even after dormancy the connection remains strong. This explains why *Narcissus* bulbs in

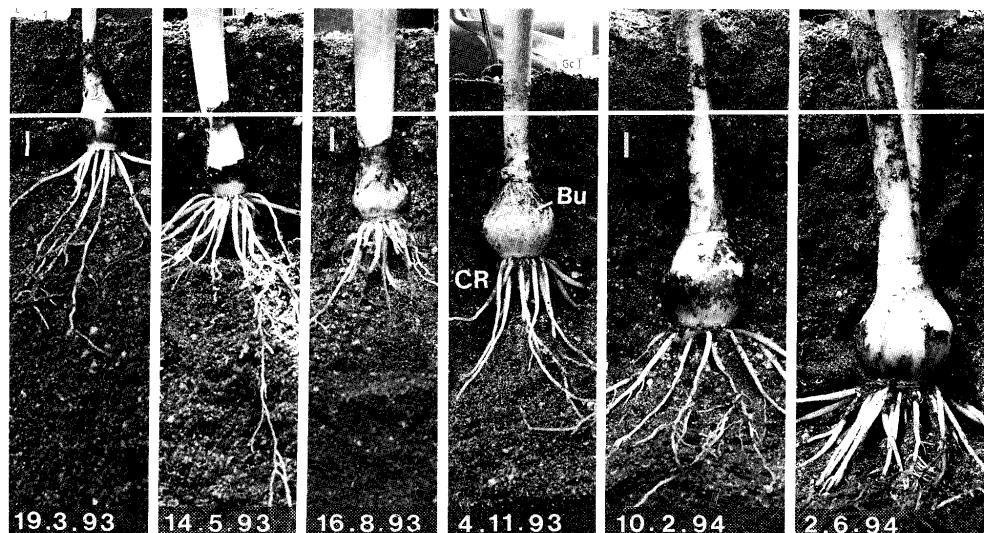


Fig. 1. *Galtonia candicans*: underground movement as time lapse photography. Date of examination is given in the lower section of each photo. White control line results from the control mark. Bars represent 10 mm. Bu bulb, CR contractile roots.

nature are often found in larger aggregates of bulbs. However, aggregates of bulbs also result in a large increase in soil resistance, and it can be supposed that further movement becomes slower and finally stops.

There are large differences between bulbs with and without light illumination on the leaf base (L+ and L-). Shallowly planted bulbs (L+) of *Nothoscordum* (see Fig. 3) developed roots at the base, which were visibly wrinkled at the surface (Wr) showing that they are involved in contraction. This wrinkling appeared in the proximal root parts over a length of at least 40 mm. The proximal roots parts swelled approx. 3 mm in *Nothoscordum inodorum* and more than 6 mm in *Narcissus tazetta* (see Table 1). The shape of the bulbs could be described as oval or elliptical (see Fig. 3 A, B).

In species without illumination (L-) the shape of the bulb changed, becoming more globular (Fig. 3 C, D). The bulb base elongated a few millimeters (EL in Fig. 3). The bulb diameter in both species increased in deeply positioned individuals, e.g. in *Nothoscordum* approx. 20–30%, but this increase is not significant. However, the L- individuals produced roots which were significantly smaller (approx. 1 mm) than those of the L+ plants, and showed no real features of contraction²).

²) A few of these roots show some wrinkles at the root surface of the proximal root part over a length of approx. 10 mm.

The morphological differences due to different light conditions are not produced by temperature conditions, e.g.: L- plants at constant temperature (T0) had the same features as L- plants which had grown with temperature changes (T15 in Table 1). The same applies in the case of L+ plants (Table 1).

Discussion

Our time lapse photography shows for the first time the vertically downward movement of bulbs, which we described as typical bulb movement (PÜTZ 1991). Very similar bulb movements can also be reconstructed from a few descriptions, e.g. by RIMBACH (1898 a) for *Lilium martagon*, by WOODHEAD (1904) for *Scilla festalis* or by RIMBACH (1938) for *Phaedranassa chloracea*. Tilting and twisting, as we have described for *Nothoscordum inodorum* bulbs (PÜTZ 1993) seem to be common to

This indicates that the roots still have the ability to contract. Although it can be stated that the pulling effect of these few roots must be near zero, the significance of these wrinkles should be taken into consideration in further investigations. We made some handcuts through these roots but could not find the anatomical features which are typical for root contraction (expansion and collapse of cortical cells, e.g. see JERNSTEDT 1984 or PÜTZ & FROEBE 1995).

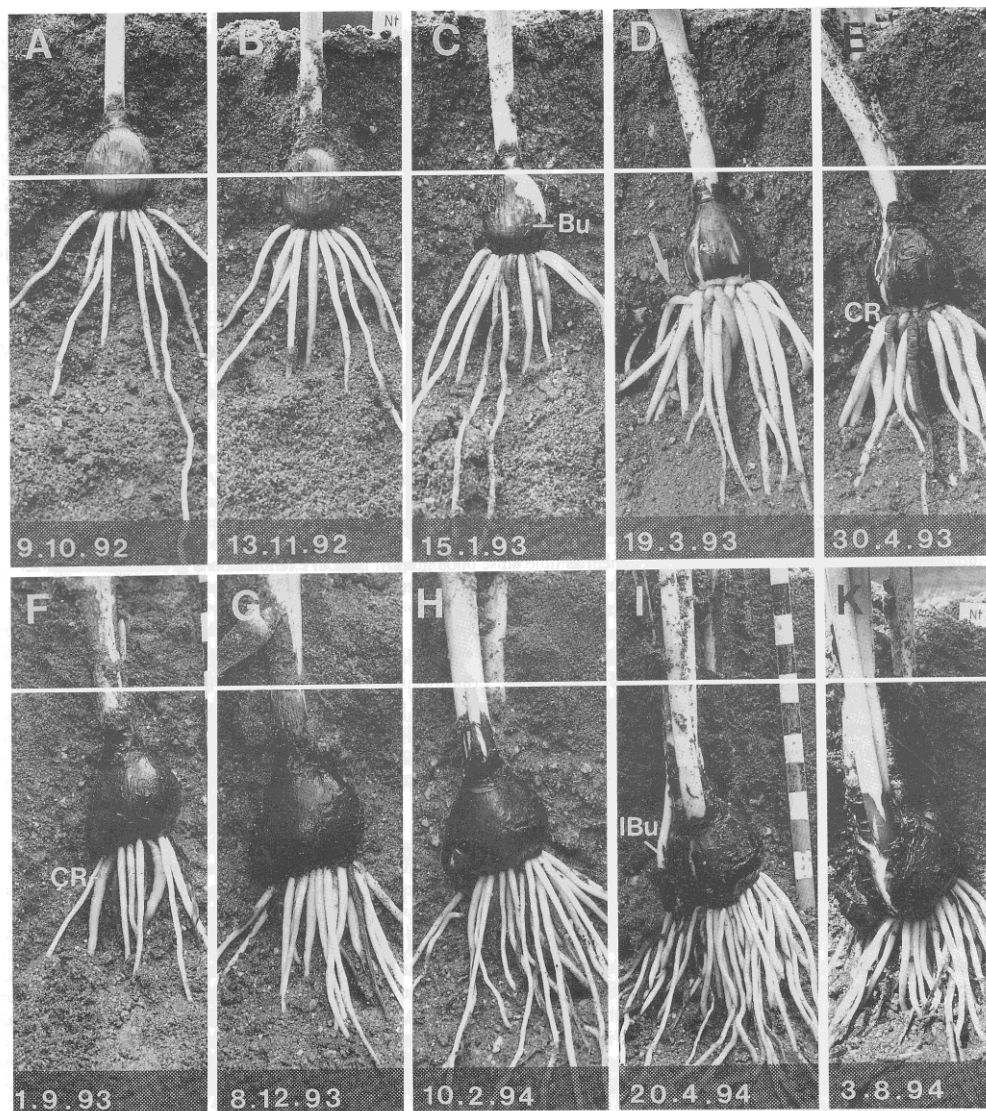


Fig. 2. *Narcissus tazetta*: underground movement as time lapse photography. A–E: movement in the first vegetation period, F–K: movement in the second vegetation period after dormancy. Date of examination is given in the lower section of each photo. White control line results from the control mark. Bars represent 10 mm. Bu bulb, l Bu lateral bulb, CR contractile roots. Arrow shows secondary change of the course of an old contractile root by the continuous bulb movement.

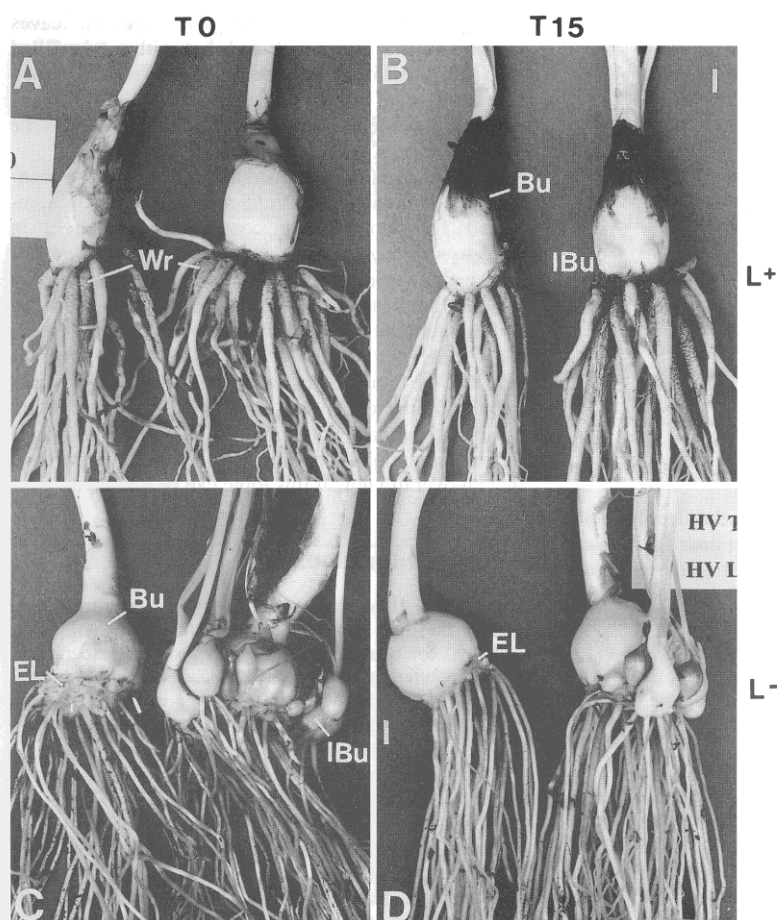


Fig. 3. *Nothoscordum inodorum*: shallow (A and B) and deep (C and D) planted individuals three month after sprouting. Plants in A and C were grown at constant temperature (T0), plants in B and D were grown at day-night temperature changes of 10–20 °C (T15). Bars represent 10mm. Bu Bulb, l Bu lateral bulb, Wr wrinkling of the root surface, EL elongation of the bulb base.

only a few bulb species in increasing the channel effect. This channel effect plays an important role in the activity of contractile roots as moving organs. Contractile roots not only create a pulling force, but also push the soil away laterally and form a soil channel in which movement is made easier (FROEBE & PÜTZ 1988). This channel effect can be calculated in % steps (PÜTZ 1992), i.e. a plant having a 100% channel effect can move without any soil resistance, a plant having a 0% channel effect has to overcome the total soil resistance. We have made some experiments to compare the energy expenditure of pulling and pushing (PÜTZ et al. 1995), and found root channel formation to be always advantageous in movement. Furthermore, we have been able to

show that for smaller movements (20–30 mm) creating only a small channel (10–40%) is most efficient. Thus, it is clear that most bulbous plants which have such a small movement also form only a small channel. In *Galtonia candicans* and *Narcissus tazetta*, the channel effect is calculated as being 10–20%. However, there are some indications that plants having located their underground organ near the soil surface are able to increase their channel effect, partly by increasing the root diameter (*Phaedranassa chloracea*, RIMBACH 1938), and partly by reducing the diameter of the bulb or corm (*Crocus sativus*, NEGBI et al. 1989). Both effects also occur in *Nothoscordum* and *Narcissus*: the deeply planted bulbs (L–) are more globular and have very

Table 1. Diameter and number of contractile roots, and bulb diameter related to the different culture conditions. Data of root number, and bulb diameter represent the average for each 10 individuals. Data for the root diameter (in mm) represent the average of 100 roots (10 roots each of every individual were measured). (For abbreviations see materials and methods.)

	<i>Nothoscordum inodorum</i>			<i>Narcissus tazetta</i>		
	bulb dia- meter	root num- ber	root dia- meter	bulb dia- meter	root num- ber	root dia- meter
T 15 L+	15 ± 3	24 ± 9	3,1 ± 0,3	26 ± 8	14 ± 4	6,4 ± 0,8
T 0 L+	16 ± 2	28 ± 8	3,2 ± 0,5	28 ± 6	16 ± 5	5,9 ± 0,7
T 15 L-	19 ± 2	25 ± 6	1,3 ± 0,2	32 ± 4	18 ± 5	1,8 ± 0,4
T 0 L-	22 ± 4	31 ± 9	1,0 ± 0,3	33 ± 5	20 ± 4	1,9 ± 0,3

small roots, while the shallow ones are egg-shaped and of smaller diameter (see Table 1), while produces larger roots (Fig. 3).

Our observations also demonstrate that deeply planted individuals of several species register their position and, if satisfactory, produce no more contractile roots (e.g., RIMBACH 1897, 1897a, 1938; KIRCHNER et al. 1934; IZIRO & HORI 1983; HALEVY 1986). There are many parameters possibly used by plants in detecting their depth:

- (1) light
- (2) temperature
- (3) conditions of the previous vegetation period
- (4) soil gradients of chemical compounds (O₂, H₂O or CO₂).

GALIL (1958) was the first to make experiments in this field and found rapid soil temperature changes to be the reason for the induction of special contractile root formation in *Leopoldia maritima*. Rapid soil temperature changes, together with light illumination of the sheath leaves, were identified for *Gladiolus* (JACOBY & HALEVY 1971; HALEVY 1986) as the cause of contractile root formation. However, these workers only took account of light and temperature [(1)+(2)] during the vegetation period. Our preliminary experiments here described were carried out under quasi natural conditions and took account of all parameters:

Regarding (1)+(2): we cultivated the plants under defined conditions, with and without light illumination, and with and without temperature fluctuations (see Table 1).

Regarding (3): we selected plants which had grown in shallow soil positions in the previous vegetation period. Any pre-induction of contractile root activity would have made our results unclear: even deeply positioned plants would have been expected to show some contraction activity.

Regarding (4): soil gradients of various chemical compounds (e.g. O₂, H₂O or CO₂) have been taken

account of in our experiments by protecting the leaves from illumination not with soil, but with a tube filled with small (3–5 mm), dry beads of black foam rubber. The absence of compound gradients in the tubes excludes any influence of such gradients on the contractile activity of roots.

Thus, our results demonstrate that temperature changes, pre-induction and gradients of chemical compounds have no effect on contractile root activity in *Nothoscordum inodorum* and *Narcissus tazetta*. The only parameter responsible for contractile root activity is light illumination on the basal leaf parts.

Summarizing our results with those of GALIL (1958), JACOBY & HALEVY (1970) and HALEVY (1986), it can be said that the induction of contractile root activity varies greatly in different species, perhaps due to variation in ecological habitats. Further investigation should include field examination of the natural habitat of the species so that an overall view of this topic can be obtained.

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Buchbesprechung

OBERDORFER, E.: **Lebenserinnerungen des Pflanzensoziologen E. O.** – Jena, Stuttgart: Gustav Fischer Verlag 1995. – 94 S., 13 Abb., kt. DM 28.–. ISBN 3-334-61004-7

Wenn ERICH OBERDORFER am Ende seines beruflich und familiär erfüllten Lebens seine Memoiren schreibt, so bedeutet das einen Gewinn für alle, die seinen Lebensweg begleitet haben oder ihm bei gemeinsamen wissenschaftlichen Anliegen nahegekommen sind. Mit dem Namen ERICH OBERDORFER verbinden sich für alle Vegetationskundler des deutschsprachigen Raums wie darüber hinaus wichtige Fortschritte auf dem Gebiet der von BRAUN-BLANQUET begründeten pflanzensoziologischen Schule bei der Erarbeitung eines umfassenden Systems der Pflanzengesellschaften auf regionaler Basis. Innerhalb des sich bei der Weiterentwicklung der BRAUN-BLANQUETSchen Lehre während der zurückliegenden Jahrzehnte herausbildenden wissenschaftlichen Spannungsfeldes zwischen unterschiedlichen Arbeitsrichtungen, wofür nur Namen wie TÜXEN, AICHINGER und SCAMONI genannt seien, kommt dem Schaffen von OBERDORFER eine zentrale Stellung zu. Ausdruck dessen ist die hohe Anerkennung, die die von ihm und seinen Mitarbeitern zur Flora und Vegetation vor allem des süddeutschen Raumes geschaffenen Werke mit deren Aussagekraft weit über dessen Grenzen hinaus finden.

Beeindruckend ist es aus heutiger Sicht, mit den Augen des Autors noch einmal den steinigen Weg mitzuverfolgen, der in den Jahren nach dem 2. Weltkrieg in zunehmenden Maße dazu

führte, die grundlegenden Erkenntnisse der pflanzensoziologischen Lehre in praxisrelevante Aufgabenstellungen einzubeziehen und erfolgreich auf den verschiedensten Anwendungsgebieten in Praxis wie Administration als integrierten Bestandteil entsprechender Vorhaben zum Tragen zu bringen.

Die Memoiren machen sichtbar, wie es OBERDORFER verstand, so unterschiedliche Aufgaben wie die eines Hochschullehrers, angewandt arbeitenden Pflanzensoziologen und begeisterten Sammlers und Museologen miteinander zu verbinden, ohne sich darüber den familiären Anliegen und Problemen, was besonders für die schwierigen Nachkriegsjahre gilt, weniger nachdrücklich zu widmen.

Wer die Memoiren OBERDORFERS liest, wird aus heutiger Sicht vielleicht einige seiner persönlichen Entscheidungen nicht ohne weiteres verstehen können. Das, was man aber uneingeschränkt anerkennen sollte, ist die Offenheit, mit der über manche der dem Verfasser sicher nicht leicht gewordenen Schritte berichtet wird. Dies beeindruckt als eine selbstkritische Haltung, die leider nicht bei allen Memoirenschreibern in gleicher Weise zu finden ist.

So bildet das kleine Büchlein eine interessante, lesenswerte Lektüre, die uns nicht nur den Verfasser selbst mit seiner starken Ausstrahlungskraft, sondern zugleich auch manchen, der auf die Entwicklung der Vegetationskunde während der letzten Jahrzehnte Einfluß nahm, aus der Sicht OBERDORFERS in sehr persönlicher Weise nahebringt.

E.-G. MAHN Halle (Saale)

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