MEETINGS OF THE ROYAL BOTANICAL SOCIETY OF THE NETHERLANDS

MEETING OF THE SECTION FOR PLANT MORPHOLOGY AND ANATOMY ON NOVEMBER 19, 1971

P. BAAS (*Rijksherbarium, Leiden*)

Anatomy and affinities of Hua Pierre and Afrostyrax Perkins and Gilg

Fruit and seed structure, vegetative anatomy and pollen morphology of *Hua* and *Afrostyrax* have been studied in order to elucidate the taxonomic affinities of these enigmatic genera from tropical West Africa. *Hua* was initially described in the *Sterculiaceae* and *Afrostyrax* in the *Styracaceae*. Various authors have since then put forward a number of suggestions about the taxonomic affinities, including presence or absence of mutual relationships between the genera and affinities to the *Sterculiaceae*, *Styracaceae*, *Linaceae s.l.*, *Dipterocarpaceae*, *Tiliaceae*, or *Erythroxylaceae*. Micromorphological characters strongly support the mutual affinities of the two genera. The common characters are: Fruit wall with outer and inner parenchymatous layers separated by a layer of stone cells. Outer testa parenchymatous, supplied with vascular bundles. Inner testa with an outer sclerenchymatous palisade layer, arising from the outer epidermis of the inner integument. Pollen triporate and operculate. Stomata paracytic. Petiole supplied with cylindrical vascular system enclosing medullary bundle(s). Venation pattern of regularly arranged veinlets enclosing rectangular areoles. Extrafloral nectaries with palisade-like epidermis mostly present. Cristarque cells present in ground tissue of petiole and stem. Node 3-trace, 3-lacunar. Bark enclosed by solid perivascular sclerenchyma ring, traversed by narrow and broad, triangular rays. Wood composed of vessels with simple perforations and alternate wall pitting, libriform fibres, banded paratracheal parenchyma and heterogeneous broad and narrow rays. This complex of characters excludes *Styracaceae*, *Erythroxylaceae*, *Dipterocarpaceae*, *Tiliaceae*, and *Linaceae* as close relatives of *Hua* and *Afrostyrax*. Out of 50 families studied in the comparisons *Sterculiaceae* and *Bombacaceae* appear to show most resemblance in anatomical features, but are sufficiently different in e.g. their possession of mucilage cells or cavities, stratified phloem and more advanced xylem to justify family status for *Huaceae*, including both *Hua* and *Afrostyrax*. The inclusion of *Huaceae* in *Malvales* seems justified as was suggested by of a number of previous authors. A full account of the anatomy and a discussion of the affinities of *Huaceae* has been published in Blumea 20(1), 1972.

L. GOOSEN-DE ROO (*Botanisch Laboratorium, Leiden*)

A submicroscopical study of the formation of secondary cell wall thickenings in tracheary elements of Cucumis sativus L.

The relation between the formation of the secondary wall-sculpture and the population of cell organelles was investigated in tracheary elements of the hypocotyl of *Cucumis sativus* L.

   The sizes of thickenings in either radial or approximately radial sections of xylem elements, were arbitrarily divided into five categories:

Category 0 no thickenings
Category 1 size of thickening $\leqslant 1\mu^2$

Category 2 size of thickening $>1\mu^2$ and $<2\mu^2$
Category 3 size of thickening $>2\mu^2$
Category 4 fully developed thickenings, no protoplasm left.

These categories are assumed to correspond with successive stages of differentiation. Furthermore, the densities of the cell organelles measured in number of organelles per μ^2 in the vicinity of the thickening have been compared in the five categories. Because of their possible role in the deposition of cell wall substances, special attention was paid to the distribution of the endoplasmic reticulum and the vesicles of the Golgi apparatus (PORTER 1961; PICKETT-HEAPS & NORTHCOTE 1966). The obtained data show that the density of the endoplasmic reticulum in category 2 is significantly higher than in the categories 1 and 3, whereas the density of Golgi vesicles in category 2 is less, although not significantly, than in the categories 1 and 3. The possible relation between these distributions and the deposition of cell wall material needed for the thickenings has been considered.

Besides, we studied the distribution of cell organelles within the various categories, comparing the organel densities in the cytoplasm between the developing cell wall thickenings and in the cytoplasm facing the thickening bands. In category 2 the density of endoplasmic reticulum appeared to be uneven: the density in the assumed zones of deposition of thickening material was significantly lower than the densities in the areas between the thickenings. The vesicles of the Golgi apparatus had a similar distribution in the first category of cell wall thickening development. WOODING & NORTHCOTE (1964) and HEPLER & FOSKET (1971) reported a typical distribution of microtubules near the cell wall in xylem elements. However, the present results indicate that the observed concentration of endoplasmic reticulum and Golgi vesicles may also be responsible in certain stages of differentiation for the optical patterns on the surface of the protoplast in differentiating tracheary elements observed under the light microscope by CRÜGER (1855), DIPPEL (1867), and SINNOTT & BLOCH (1945).

CRÜGER, H. (1855): Zur Entwicklungsgeschichte der Zellenwand. *Bot. Zeitung* 13: 601–613; 617–629.
DIPPEL, L. (1867): Die Entstehung der wandständigen Protoplasmaströmchen. *Abhandl. Naturforsch. Gesellsch. Halle* 10: 53–68.
HEPLER, P. K. & D. E. FOSKET (1971): The role of microtubules in vessel member differentiation in Coleus. *Protoplasma* 72: 213–236.
PICKETT-HEAPS, J. D. & D. H. NORTHCOTE (1966): Relationship of cellular organelles to the formation and development of the plant cell wall. *J. Exp. Bot.* 17: 20–26.
PORTER, K. R. (1961): The endoplasmic reticulum: some current interpretations of its forms and functions. In *"Biological structure and function"* Ed. GOODWIN & LINDBERG, New York, London, Academic Press: 127–155.
SINNOTT, E. W. & R. BLOCH (1945): The cytoplasmic basis of intercellular patterns in vascular differentiation. *Amer. J. Bot.* 32: 151–156.
WOODING, F. B. P. & D. H. NORTHCOTE (1964): The development of the secondary wall of the xylem in Acer pseudoplatanus. *J. Cell Biol.* 23: 327–337.

SYMPOSIUM MORPHOLOGY AND ANATOMY

SECOND SYMPOSIUM MORPHOLOGY AND ANATOMY (ZWEITE MORPHO-
LOGEN-TAGUNG). JOINT MEETING OF THE SECTION FOR PLANT MOR-
PHOLOGY AND ANATOMY, AND THE SECTION FOR MORPHOLOGY AND
SYSTEMATICS OF THE GERMAN BOTANICAL SOCIETY (DEUTSCHE BO-
TANISCHE GESELLSCHAFT), HELD AT NIJMEGEN ON 28 FEBRUARY AND
1-2 MARCH 1973.

W. A. VAN HEEL (*Rijksherbarium, Leiden*)

The gynoecium of Scaphocalyx (Flacourtiaceae)

The pistil is an urceolate box issuing into 5–7 spoon-shaped stigmas. In it are two whorls of
ovules along the wall, the lower whorl in the same planes as are the stigmas, the upper whorl
in alternate radii. The ovules are sessile and atropous; they have two integuments which both
terminate in 2 or 4 lobes or projections. The ovules become seeds chiefly by means of a curious
proximal reniform growth. Lobes of the endocarp grow around the ectostome. The testa is
formed in an intercalary way below the two integuments, it has its hard layer in the middle.
The seeds consist of two parts, a hard container containing an endospermic body that lies free
inside. The outer cell layers of this body are formed by the inner cell layers of the testa that
become separated from the hard part. There is a peculiar vascular bundle pattern. It is thought
that this Malaysian monotype could be a relic species, showing a number of Gymnospermous
peculiarities. Its structure does not concord with the classical views on carpels. To replace the
classical model, as well as the deductive phylogenetic reasoning, an inductive method must be
adopted in the study of floral structures.
To be published in Blumea 21(2), 1973

ROLF SATTLER (*Biology Department, McGill University, Montreal*)

Gynoecial morphology. Conceptual aspects

It is shown that in addition to carpellate gynoecia various kinds of acarpellate gynoecia occur,
i.e. gynoecia to which the carpel concept cannot be applied. Hence the carpel concept, al-
though useful, is only of limited applicability. Angiosperms cannot be defined by the possession
of carpels. To cope with the whole diversity of gynoecial construction it is proposed to use the
concepts "gynoecial primordium", "gynoecial appendage", "placenta", "ovule" and "mega-
sporangium". A gynoecial appendage develops from a gynoecial primordium, the latter being
a structure which forms the whole gynoecium or part of it except the placentae and ovules.
Evolutionary changes of the gynoecium are visualized by the following processes:

1. Change of the relative position of primordial inception, 2. Temporal change of primordial inception, 3. Intercalation, 4. Postgenital fusion, 5. Reduction, 6. Amplification, 7. Modification, 8. Transference of function.

Different gynoecia result depending on which of these processes or which combination of these processes have occurred. The carpellate gynoecium is but one possibility among all the others like gynoecia with terminal or axillary placentation, acarpellate inferior ovaries, etc. – The statement that only some Angiosperms have carpels does not imply any phylogenetic interpretation.

However, phylogenetic speculations can be based on the description by means of the proposed conceptual framework. For example, it can be assumed that all taxa with acarpellate gynoecia evolved from carpellate taxa. But the framework could also be used to state that only some of the acarpellate taxa evolved from carpellate ones, or even that some or all of the carpellate taxa evolved from acarpellate ones. – Advantages of the proposed conceptual framework over existing ones are the following:

1. It is based exclusively on developmental data which include the mature structure as a final stage. 2. Therefore, it is hologenetically meaningful. 3. It eliminates the concept of "congenital fusion" and other non-developmental and non-hologenetic concepts. 4. Consequently, it puts comparative gynoecial morphology on an empirical basis which is more objective and more exhaustive and provides a sounder background for phylogenetic speculations.

LUTZ BUNNIGER (*Botanisches Institut Justus Liebig Universität, Giessen*)

Studies on the morphological origin of the hypanthium in Myrtales and Thymelaeales

Morphologic-histogenetic investigations of Onagraceous, Myrtaceous and Thymelaeaceous flowers have revealed that all the species dealt with pass through a stage of "meristem-plug" and "ring-shaped torus" during early ontogenesis. All the primordia of the flower organs originate in the subdermal layer. The floral tube (hypanthium) of the Myrtaceous and Thymelaeaceous flowers should be regarded as an axial organ. In the case of the former, as in Onagraceous flowers, the inferior ovary is lined on the inside by carpel tissue and is enclosed by axis tissue; both tissues differ in the nature of their cells.

The development of the flowers of all three families is described. Since the hypanthium in the Thymelaeaceous flower we examined and in the families of Myrtales we investigated is of an axis nature this difference which up to now has been said to be a characteristic of differential diagnosis, can no longer be considered relevant to the discussion on the connection between the two related groups.

BUNNIGER, L. (1972): *Beitr. Biol. Pflanzen* 48: 79–156.

KWITON JONG (*Department of Botany, University of Aberdeen, Scotland*)

Streptocarpus (Gesneriaceae) and the phyllomorph concept

Streptocarpus Lindl. subgenus Streptocarpus contains a wide variety of unusual growth forms whose morphological organisation does not conform to the standard pattern of stem, leaf, and axillary shoot.

Developmental studies in representatives of several of the growth forms have revealed that

the variation is centred around a leaf-like unit, the *phyllomorph*. It is an integrated entity that combines characteristics of both stem and leaf. It consists of a foliose component, the *lamina* which has the capacity for continued growth, and a rooting petiole-like stalk, the *petiolode* which possesses certain shoot attributes. The morphogenetically significant region of a phyllomorph is the lamina-petiolode junction where three *persistent meristems* are located. Two of these are *intercalary meristems* responsible for intercalary growth, while a third one, the *groove meristem*, which often shows cytohistological properties of a conventional shoot apical meristem, is the source of additional phyllomorph primordia, and ultimately of inflorescence primordia.

The phyllomorph concept makes possible the adequate and accurate description of the diverse growth patterns studied so that their interrelationship could be appreciated while at the same time highlighting points of morphological and morphogenetic interest. The diversity is associated with the well-known phenomenon of unequal growth of the cotyledons shortly after germination.

The first or *cotyledonary* phyllomorph of the plant is that which develops from an enlarged cotyledon. In unifoliate forms no further phyllomorphs are produced, hence the whole plant is a single phyllomorph. Other more complex growth forms are composed of additional phyllomorphs which repeat the morphological pattern of the cotyledonary phyllomorph (bypassing of course the cotyledon stage).

A remarkable plurifoliate species, *Streptocarpus fanniniae*, is considered in some detail to demonstrate the nature of the developmental complexity and morphological unorthodoxy that occurs in the subgenus.

PETER LEINS (*Institut für Systematische Botanik, München*)

Weitere Untersuchungen zur Polyandrie

Es können drei Typen multistaminater Androeceen unterschieden werden.

1. Echt polymeres Androeceum: Es besteht aus zahlreichen einfachen Organen (Stamina), die sich in die normale akropetale Sukzession aller Blütenglieder einfügen (Magnoliidae).
2. Androeceum mit sekundär eingeschobenen einfachen Organen: Die Polymerie durch Einschiebung neuer Stamina steht im Zusammenhang mit einer Vergrößerung des Blütenbodens. Man kann zwischen kollateraler (Alismataceae), zentrifugaler (*Hydrocleis*) und zentripetaler Einschiebung (Rosaceae) unterscheiden (LEINS u. STADLER, im Druck; KANIA, im Druck).
3. Androeceum mit komplexen Organen (LEINS 1971): Die zahlreichen Stamina sind nur Teile weniger (ein- oder zweikreisig angeordneter) komplexer Organe.

Die Primordialhöcker komplexer Organe sind meist dreieckig. Die Anlage der Einzelstamina beginnt an der Spitze des Primordialhöckers mit einem Primordium und schreitet – entweder am Rand oder auf der Ventralseite (*Philadelphus*, Myrtaceae) oder Dorsalseite (Dilleniidae, Caryophyllidae) – basalwärts fort; bei Aufgliederung der gesamten Ventral – oder Dorsalfläche vergrößert sich naturgemäß die Zahl der Stamina nach unten zu. Abweichend entwickeln sich die epipetalen komplexen Organe mancher Loasaceae (*Loasa, Blumenbachia, Cajophora*): Die "zentrifugalen" Stamina sind hier in zwei Doppelreihen angeordnet.

KANIA, W.: Entwicklungsgeschichtliche Untersuchungen an Rosaceenblüten. *Bot. Jb.*, im Druck.

LEINS, P. (1971): Das Androeceum der Dikotylen. *Ber. Dtsch. Bot. Ges.* **84**: 191–193.

LEINS, P. und P. STADLER: Entwicklungsgeschichtliche Untersuchungen am Androeceum der Alismatales. *Österr. Bot. Z.*, im Druck.

J. H. BOEKE (*Biologisch Centrum, Rijksuniversiteit Groningen, Haren*)

Postgenitale Verwachsungen im Gynoeceum von Trifolium repens

Die Ränder des monokarpellären Gynoeceums der Leguminosen verwachsen postgenital mit einander. Bei *Trifolium repens* berühren die Epidermiszellen der Karpellränder einander schon zu einem frühen Zeitpunkt der Ontogenie und verwachsen danach lückenlos. Periklinale Teilungen in den subdermalen und in den verwachsenen dermalen Schichten, sowie die Differenzierung der Funiculi und der ventralen Gefässe verzerren die ursprüngliche Anordnung der Zellen. Durch histogenetische Analyse von Serienschnitten verschiedener Entwicklungsstadien kann jedoch die Nahtlinie zwischen den Karpellrändern sogar in alten Stadien abgeleitet werden.

Elektronenmikroskopische Bilder zeigen, daß schon vor der Verwachsung die Epidermis der Karpellränder mit einer Kutikula bedeckt ist, die lichtmikroskopisch nicht nachweisbar ist. Nach der Verwachsung zerfallen die eingeschlossenen Kutikulas in kleine Fragmente, die die Nahtlinie markieren. Die unter der Kutikula liegenden Pektinschichten vereinigen sich dann zu einer Schicht, die einer Mittellamelle ähnelt.

Die ausführlichen Resultate der Untersuchungen werden demnächst in Acta Botanica Neerlandica veröffentlicht.

A. D. J. MEEUSE (*Hugo de Vrieslaboratorium, Amsterdam*)

Neomorphologie und Angiospermenphylogenie

Phylogenetische Morphologie unterscheidet sich von klassisch-topologischen Theorien in mancherlei Hinsicht. Ein Beispiel wurde gegeben das in den historisch-ökologischen Betrachtungen eine große Rolle spielt. Es handelt sich hier um Fragen bezüglich der Herkunft des Andrözeums der Angiospermen. Eine "Ableitung" der blattartigen magnolioiden Staubblätter von mesozoischen Vorläufern und ein divergentes Entstehen der Staubblätter mit Staubfäden zusammen mit einem Perianthglied (öfters als Semaphyll entwickelt) aus demselben Prototypus wird vorgeschlagen. Magnolioide Angiospermen können deswegen unmöglich der Ahnentypus der anderen Gruppen der Angiospermen darstellen.

MEEUSE, A. D. J. (1972): *Acta Biotheor.* **21**: 145–166.

O. ROHWEDER (*Institut für systematische Botanik, Universität Zürich*)

Angiospermen-Morphologie auf phylogenetischer Grundlage?

Es ist heute nicht mehr die Frage, ob eine phylogenetisch begründete Angiospermen-Morphologie berechtigt, sondern ob sie möglich ist. Voraussetzungen für ihre Realisierung sind: 1. Genaue und sichere Kenntnis der Fossilien, die als Ahnenformen in Frage kommen. 2. Hinreichende Wahrscheinlichkeit enger sippenphylogenetischer Beziehungen zwischen vermuteten Stammformen und Angiospermen. 3. Identifizierbarkeit der Angiospermen-Organe mit denen der potentiellen Vorfahren. Diese Bedingungen sind nicht erfüllt. Rekonstruktionen fossiler Pflanzen sind selbst in hohem Maße hypothetisch, wie zahlreiche drastische Neuinterpretationen der letzten Zeit beweisen. Es gibt in den Jura- und Trias-Formationen keine Spermatophyten, die aufgrund genügender Aehnlichkeit oder mit Hilfe von Zwischenformen als Vorfahren der Angiospermen oder deren nahe Verwandte erkannt werden könnten; es muß vielmehr damit gerechnet werden, daß die Stammformen nicht unter den bekannten Fossilien

sind. Die an sich denkbare Verknüpfung mit paläozoischen Gruppen wie den Pteridospermen bringt keine Klärung, da Anhaltspunkte fehlen, welche Angiospermen-Organe aus welchen Organen dieser frühen Spermatophyten hervorgegangen sein könnten. Das gilt auch für die Cupula, von der sich nicht einmal sagen läßt, ob bei den Angiospermen ein Homologon existiert. Unser derzeitiges paläobotanisches Wissen läßt einen breiten Spielraum für zahlreiche einander widersprechende Hypothesen, die weder verifizierbar noch falsifizierbar sind; es kann daher eher die "angiosperm centred morphology" als Maßstab für die Wahrscheinlichkeit phylogenetischer Hypothesen dienen, als daß sich die Angiospermen-Morphologie auf solche Hypothesen begründen ließe.

ROHWEDER, O. (1973): Angiospermen-Morphologie – Ergebnis oder Ausgangspunkt phylogenetischer Hypothesen? *Bot. Jahrb. Syst.* 93: im Druck.

F. WEBERLING (*Botanisches Institut Justus Liebig Universität, Giessen*)

Über die Beziehungen zwischen Vaginalloben und Stipeln

Scheidenlappen (Domin) oder Vaginalloben entstehen während der Blattentwicklung durch allmähliche, oft in unterschiedlichem Maße hervortretende Ausweitung der oberen Scheidenränder. Sie lassen sich allgemein gut von den frühzeitig und konstant auftretenden, proleptisch sich weiterentwickelnden Stipeln unterscheiden. Bisweilen verstärkt sich die Ausweitung der Scheidenränder in der Blattfolge und erfolgt zunehmend früher – teilweise infolge eines intensiveren Randwachstums. Bei einzelnen Sippen einiger Familien (Ranunculaceae, Berberidaceae, Saxifragaceae, Umbelliferae u.a.), in denen Scheidenlappen vorkommen, erscheinen sie so früh und zeigen eine so deutliche Prolepsis, daß man nicht mehr zwischen Vaginalloben und Stipeln unterscheiden kann. Dies eröffnet die Möglichkeit einer morphologischen (vielleicht auch phylogenetischen) Ableitung der Stipeln.

HANS-DIETER IHLENFELDT (*Institut für Allgemeine Botanik, Hamburg*)

Über die Entstehung der Kräuter bei den Angiospermen

Die meisten phylogenetisch orientierten Systematiker vertreten heute die Ansicht, daß bei den Angiospermen der krautige Habitus aus dem holzigen (baumförmigen) Habitus sekundär entstanden ist. Eine kritische Analyse der bisher vorgelegten Theorien zeigt, daß eine ganze Reihe von phylogenetischen Prozessen, die einzeln oder kombiniert auftreten können, an der Entstehung der krautigen Achse beteiligt waren. Aufgrund einiger bislang vernachläßigter Befunde (zeitliche Staffelung der Leitbündelinduktion und damit gekoppelt Auftreten von "unvollständigen" Leitbündeln) werden die breiten Markstrahlen der Eustele, deren Entstehung bislang nur unbefriedigend erklärt werden konnte, als das Ergebnis einer fortschreitenden basalen ontogenetischen Abbreviation der Leitbündeldifferenzierung gedeutet.

ALBERTA M. W. MENNEGA and JIFKE KOEK-NOORMAN (*Instituut voor Systematische Plantkunde, Utrecht*)

A comparison of the wood structure of the Rubiaceae and Loganiaceae in relation to the taxonomic position of the genera Gaertnera and Pagamea

The wood anatomy of the Loganiaceae sensu Leenhouts (Flora Malesiana Ser. I, vol. 6²:

293. 1962) comprising the tribes Potalieae, Buddlejeae, Antonieae, Gelsemieae, Strychneae, Loganieae, and Spigelieae, is very heterogeneous. Nearly every feature, with the exception of scalariform perforations of the vessels, may be present in one genus or another. The inclusion of the Buddlejeae implies furthermore that the family is no longer characterized by the presence of intraxylary phloem.

The genera *Gaertnera* and *Pagamea*, which are remarkably alike in wood structure, lack intraxylary phloem. As their secondary xylem does not resemble any of the genera of the Loganiaceae, incorporation in this family would enhance its diversity and introduce as an additional character the presence of raphides.

From an anatomical point of view the Rubiaceae are much more homogeneous. All features characteristic for *Gaertnera* and *Pagamea* occur in one or more subfamilies of the Rubiaceae. The two genera differ from *Psychotria* and nearest allies by the presence of fibre tracheids and broad apotracheal parenchyma bands. However, elsewhere in the subfamily Rubioideae this combination of characters does occur, as well as the raphide bundles. Wood anatomy therefore supports Bremekamp's concept of placing *Gaertnera* and *Pagamea* in a separate tribe within the Rubioideae.

KOEK-NOORMAN, J. (1969): A contribution to the wood anatomy of South American Rubiaceae. II. *Acta Bot.Neerl.* 18: 377–395.
MENNEGA, A. M. W. Wood Anatomy of the Loganiaceae, to be published in A. J. M. LEEUWENBERG's treatment of the Loganiaceae in Pflanzenfamilien, 2. Aufl.

P. BAAS (*Rijksherbarium, Leiden*)

Structural variation in the secondary xylem of seventy species of the genus Ilex

The wood of the genus *Ilex* is always characterized by vessel members with scalariform perforations, a ground tissue consisting of fibre tracheids, and heterogeneous broad and narrow rays. The parenchyma is usually scanty and diffuse. Within this framework a great deal of variation may be encountered, which is hardly or not related to subgeneric classification but to latitudinal distribution. In both the Northern and Southern hemisphere and in both the Old and New World, temperate species are characterized by conspicuous growth rings, numerous narrow vessels, relatively short vessel members, relatively few bars per perforation plate, and conspicuous spiral thickenings on both vessel and fibre walls. The tropical species, on the other hand, are characterized by the absence of clearly marked growth rings, few and broad vessels, long vessel members, many bars per perforation plate, and no or very faint spiral thickenings. The subtropical species are ususally intermediate. In only very few species important deviations from this general trend were found, which are regarded as taxonomically significant.

Comparisons with other genera and data from the literature suggest that *Ilex* follows a general trend in its correlations of vessel frequency, vessel member length, vessel diameter, spiral thickenings, and growth rings with latitude. The occurrence of more elaborate scalariform perforation plates in tropical lowland species than in temperate and tropical montane species seems to be a reversal of the general trend, however.

One may interpret the variation pattern found in different ways, which do not necessarily exclude each other. One possibility is that tropical *Ilex* species happen to have retained the more primitive characters, and that all temperate species are more derived. One may also assume that climatic conditions in general have played an important role in trends of xylem specialization. The third possibility is to regard climatic influences on the wood of *Ilex* so important in themselves that no phylogenetic significance can be attached to the variation encountered. A detailed account on the wood anatomical range in *Ilex* will be published in Blumea (1973 or 1974).

P. D. BURGGRAAF (*Botanisch Laboratorium, Leiden*)

Vessels and vessel-ends in the wood of Fraxinus excelsior L.

In the last-formed annual rings of three-year old shoots, which have developed vertically on old stumps on rather wet soil, three parts can be recognized, viz. the pore-zone, the late wood, and an intermediate zone of varying width. In this intermediate part the radial vessel diameter is intermediate between the diameter of the vessels in the pore-zone and that in the late-wood, and decreases rather slowly towards the late-wood. In wide annual rings particularly this zone is wider than in narrow annual rings.

The course of the vessels is curved or tortuous. Radial and tangential amplitudes of this course were measured (BURGGRAAF 1972). The radial amplitude is much larger in the intermediate part of the annual ring than in the pore-zone and in the late wood. The tangential amplitude does not show such differences. A three-dimensional vessel-network is present as a consequence of these curved courses, whereby vessels touch and separate again.

The number of vessels per mm^2 is much higher in the late wood, particularly in the last-formed part of it, than it is in other parts of the annual ring. This frequency is lowest in the intermediate zone.

The occurrence of blind vessel-ends has been established and studied quantitatively. These structures are called duplications and unifications when blind ending vessels are present touching another vessel, or new vessels and solitary-ending vessels when these blind ends occur without touching another vessel. The frequency of these structures, given as the number per 100 vessels present in the first of a series of transverse sections, is highest in the late wood. A high proportion (57 %) of such blind ends is due to relatively short vessels which exhibit two such ends in wood samples of 5.0 mm length. Of these short vessels 50 % is even shorter than 350 μm; they appear to consist of only one vessel-member, and, therefore, hardly deserve to be called vessels.

The results are discussed in relation to a generally accepted model of cambial activity and some discrepancies are pointed out.

BURGGRAAF, P. D. (1972): Some observations on the course of the vessels in the wood of Fraxinus excelsior L. *Acta Bot. Neerl.* 21: 32–47.

W. K. H. KARSTENS (*Botanisch Laboratorium, Leiden*)

Some aspects on the ontogenesis of certain Monocotyledonous stems

Metaxylem vessel elements of the stems of *Bambusa arundinacea, Zea mays, Saccharum officinarum* and *Cyperus alternifolius* were measured in order to obtain information on the correlation between longitudinal growth of the internodes and their anatomical structure.

Young and full-grown internodes of *Bambusa arundinacea* were investigated and the length of young and full-grown metaxylem vessel elements throughout the internodes was measured. It became clear that in the basal parts of young internodes an increasing number of very short metaxylem vessel elements is present, which cells, almost exclusively at the apical end of the intercalary zones, elongate considerably. However, a study of full-grown internodes showed distinctly that especially in the basal parts very long vessel members have differentiated. By comparing the graphs of internodes of different age and by taking the total number of cells along the internodal axis and the number of cells in the intercalary zones into account, information was gained on internodal ontogeny.

Attention was drawn to the occurrence in the investigated plants, *Bambusa* excepted, of a lenticular area at the base of the internodes in which both the peripheral and the central vascular bundles contain metaxylem elements with protoxylem-like cell wall thickenings, the

latter over a longer distance than the former; hence the lenticular shape of the concerned area.

Finally, it has been pointed out that, anatomically, the system for water transport seems to exhibit curious functional aspects.

WILLEM VAN COTTHEM (*Laboratorium voor Morfologie, Systematiek en Ecologie der Planten, Gent – Belgium*)

The classifications of morphological and ontogenetical types of stomata

Since the publication of PANT's classification of the ontogenetical types of stomata in 1965 a host of new data on the structure and development of stomata in different plant groups and families was obtained. Recently a new classification of the morphological types was made (VAN COTTHEM 1970, 1971), in which the classical number of 4 types had to be considerably enlarged, due to the discovery of several new types in ferns and angiosperms (STACE 1963, TOMLINSON 1969, PAYNE 1970 and VAN COTTHEM 1968, 1970).

Further research work and compilation of data on stomatal ontogeny led to a new classification of the ontogenetical types, in which the number of PANT's types (10) is enlarged to 26. The division into three groups is maintained (perigenous, mesoperigenous and mesogenous). Taking into consideration the ultimate structure of the adult stomata these main groups are subdivided into 6, 9, and 11 types, respectively. A modified terminology is proposed in which a combination of terms of both the morphological and ontogenetical classifications is used; by doing so the gap between the two is bridged.

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Epidermal variation and peculiarities in Winteraceae, Celastraceae and Icacinaceae

Epidermal studies using both cuticular macerations, scanning electron microscope images of intact leaf surfaces, and paradermal sections, were carried out on all species (111) of Malesian Icacinaceae, the genera *Kokoona* and *Lophopetalum* (Celastraceae), and on the majority of species of the Winteraceae.

In Malesian Icacinaceae 9 different hair types and 5 different stomatal types are present. Epidermal diversity permits identification of leaf fragments down to the genus and affords some conclusions of taxonomic importance. Correlations with wood anatomical specialization within this family provided circumstantial evidence that the anomocytic and paracytic stomatal types may be considered as primitive, and that cyclocytic stomata are most specialized.

In *Kokoona*, but particularly *Lophopetalum*, a great number of epidermal characters, such as excessive epidermal wall thickness, complexity of stomatal type, presence or absence of low papillae proved to be so variable that no characters of taxonomic or diagnostic value can be indicated in the epidermis of these genera.

In Winteraceae variability within genera and species also make taxonomic delimitation using only epidermal characters impossible. In the complex species *Drimys piperita* a number of characters are correlated with habitat. Plants from open vegetation usually have almost circular guard cell pairs, epidermal cells that are much smaller than the stomata, straight anti-

clinal walls and short and broad cells over the midrib. In forest plants the guard cell pairs are elongate and much smaller than the epidermal cells, the anticlinal walls are undulated, and the cells over the midrib are longer than broad. All intermediates between these two extremes occur.

In a majority of Winteraceae the cuticle proper is covered with an alveolar layer of cutin-like material. This alveolar material may have the form of minute or massive plugs overlying the stomatal pore and guard cells, or cover the whole lower leaf surface. Its appearance (heterogeneous or homogeneous) is extremely variable within the genera.

More detailed accounts on *Kokoona* and *Lophopetalum* and on Winteraceae will be published in Blumea (1973 and 1974); the Icacinaceae will be the subject of a paper in Acta Botanica Neerlandica (1973).

H. R. HÖSTER (*Institut für Holzbiologie und Holzschutz der Bundesforschungsanstalt für Forst- und Holzwirtschaft, Hamburg*)

Über Struktur und Entwicklung von Reaktionsgewebe bei Gymnospermen und Angiospermen

Vergleichend-anatomische und histochemische Untersuchungen am Reaktionsgewebe von Nadel- und Laubbäumen aus gemäßigten und tropischen Klimazonen zeigten eine gegenüber normalem Gewebe auffällige Veränderung der Zell- und Gewebestruktur des Xylems. Das Druckholzgewebe besitzt einen einheitlichen Aufbau aus dickwandigen und abgerundeten Tracheiden mit einer Spaltenschicht in der inneren Sekundärwand. Zugholzgewebe tritt dagegen in verschiedenen Bautypen auf und ist charakterisiert durch eine meist fehlende Lignifizierung im inneren Teil der Sekundärwand der Libriformfasern, sowie durch einen höheren Faseranteil und einen geringeren Anteil an Tracheen, die zudem englumiger sind.

Während Druckholz bei allen Gymnospermenarten auftritt, ist das Vorkommen von Zugholz auf bestimmte systematische Formenkreise der Angiospermen beschränkt. Untersuchungen am Astholz von über 400 Arten der Dikotyledonen zeigten, daß Zugholz nur dann gebildet wird, wenn das Grundgewebe des Xylems aus Fasern oder Fasertracheiden besteht. Die Differenzierung des Reaktionsgewebes wurde bei Fichte und Pappel über eine Vegetationsperiode verfolgt. Dabei konnte u.a. die Natur der ersten Frühholztracheiden im Druckholzgewebe geklärt werden.

H. B. LÜCK (*Laboratoire de Botanique analytique et Structuralisme végétal, (C.N.R.S.), Université de Provence, Centre Marseille- St. Jérôme*)

Zellproduktion und Form

Die banalen Tatsachen, daß eine Zelle sich in zwei teilt und daß ihre zwei Tochterzellen nicht zum gleichen Zeitpunkt wiederum teilungsfähig sind (Inegalität des Zustandes der Einzelzellen eines wachsenden Gewebes in bezug auf den Zeitpunkt ihrer zukünftigen Teilung) werden als wesentliche Axiome einer Modellkonstruktion verwendet. Die Werte der zwei Parameter des vorgeschlagenen Modells drücken die Vitalität und die morphologische Asymmetrie des sich entwickelnden Gewebes aus. Zwei Eigenschaften des Modells sind von besonderem morphologischen Interesse und finden ihre Adäquation im experimentell verfolgten Längenwachstum von Chaetomorpha linum Kütz. (Cladophorales): (1) Eine nach binärem Ordnungsprinzip erfolgende Unterteilung einer sich entwickelnden, durch die Zahl der sie zusammensetzenden

Zellen charakterisierten Zellfamilie*) in Teilfamilien führt zu quantifizierbaren relativen Häufigkeiten von Teilfamilien gleicher Zellzahl. Ein gegebenes, entwicklungsgeschichtlich zusammenhängendes Gewebe läßt sich dementsprechend hypothetisch in Teilfamilien aufteilen. Eine derartige Aufteilung findet ihre Analogie bei der in der klassischen Genetik üblichen Aufspaltung einer Kreuzungsnachkommenschaft in Phänotypen mit affilierten Erwartungswerten ihrer Häufigkeit. Das Arsenal der in der Genetik herangezogenen statistischen Entscheidungshilfen ist anwendbar. (2) Wird das algebraisch formulierte Modell als O-Lindenmayersprache entwickelt, ist zu jedem beliebigen Entwicklungsstadium des Gewebes die Aufeinanderfolge (Konkatenation) von Zellen und Zellgruppen höher oder niedriger Teilungsbereitschaft definierbar. Es erscheint als Modelleigenschaft, daß jede Teilgruppe beliebiger Ordnung in bezug auf die Teilungsprospektion ihrer Zellen ein Muster aufweist, das dem zu einem vorangegangenen Entwicklungsstadium vorhandenen Muster einer übergeordneten Gruppe identisch ist (Prinzip der Einschachtelung, Rekursivität, – Analogie zum biogenetischen Grundgesetz). – Anwendungsmöglichkeiten: Zelldifferenzierung bei Alterung des Gesammtgewebes, Musterbildung während der Gewebedifferenzierung (Spaltöffnungsmuster), Organverteilung (Phyllotaxis), u.a.

*) Eine Zellfamilie in einem Gewebe ist eine Gruppe von Zellen, die sich auf eine einzige Mutterzelle zurückführen lassen und untereinander in einem engeren verwandtschaftlichen Verhältnis als zu allen benachbarten Zellen stehen.

A. LINDENMAYER (*Centrale Interfaculteit, Rijksuniversiteit, Utrecht*)

Theoretical considerations of the development of compound structures

Compound plant organs, such as compound leaves, or compound branching or flowering structures, arise probably by cyclically repeated occurrences of the same sequence of developmental steps. This kind of development can be described by abstract cellular systems in which algorithmic rules give rise to each subsequent stage in the development of a particular structure. The sets of rules necessary to produce certain types of structures can be compared within a mathematical theory. Rules may also be introduced to account for interpretations among the cells. The development of compound leaves as well as of compound inflorescences will be discussed on the basis of these systems.

O. SCHÜEPP (*Reinach bei Basel, Schweiz*)

Typen der Blattverzweigung

Vergleichende Morphologie gestern, heute und morgen verbindet einfache Typen durch Metamorphose. Fiederförmige Blätter werden fingerförmig, handförmig, fußförmig. Umformung ausgewachsener Glieder durch eine Reihe von Zwischenformen kann im Film anschaulich gemacht werden. Wir denken uns *idealistisch* Formen als Verwirklichung von im Keim präformierten Urbildern. Wir verstehen *organographisch* Formen als Werkzeuge für Funktionen des Stoffwechsels und der Vermehrung, *ontogenetisch* als Ergebnis des Wachstums und betrachten sie *phylogenetisch* als Ergebnis der Stammesgeschichte. Streitfragen über die Richtung der phylogenetischen Metamorphose (fiederförmig – fußförmig oder fußförmig – fiederförmig) bleiben unbeantwortet, denn es werden in den Chromosomen nicht präformierte

Blattformen sondern Bestimmungen über den Ablauf von Wachstumsprozessen weitergegeben.

Wir brauchen heute und morgen mehr Wachstumsforschung, dazu mehr Mathematik, mehr Geometrie. Ein *Vegetationspunkt* ist mathematisch definiert Spitze des Vegetationskegels, Scheitelpunkt eines Paraboloides, Quellpunkt von welchem aus Zellen des Urmeristems ins Flankenmeristem verschoben werden. Der VP ist Zentrum einer radiären Struktur mit concentrisch angeordneten Meristemzonen. Aus der *radiären* Struktur des VK werden *dorsiventrale* Blattanlagen von sichelförmigem Umriß herausgeschnitten. Vom Blatt VP gegen die Sichelspitzen läuft eine *Vegetationslinie*, Grenze zwischen der späteren Blattober- und Unterseite, Quelle aus welcher senkrecht zum Blattrand die Blattspreite verbreitert wird. Die Punkte der VL sind Orte stärkster Krümmung der Blattoberflächen. Die VL verlängert sich durch Wachstum, krümmt sich bei der Bildung neuer Spreitenglieder. Die Blattform wird bestimmt durch das Verhältnis des Rand- zum Flächenwachstum der Spreite.

Formen sind zu beschreiben als Resultate der *Wachstumsordnung*.

W. FREY (*Institut für Biologie, Spezielle Botanik, Tübingen*)

Vergleichende entwicklungsgeschichtliche Untersuchungen an Laubmoos-blättern als Beitrag zur Systematik der Laubmoose

Die Untersuchungen umfassen die Teilungsvorgänge im Bereich der Stämmchenspitze, die Entwicklung des parenchymatischen und des prosenchymatischen Zellnetzes und die Entwicklung der Rippe des Laubmoosblattes.

Sie ergaben, daß bei allen akrokarpen Laubmoosen im Bereich der Stämmchenspitze festgelegte Teilungsvorgänge ablaufen, die von denen der pleurokarpen verschieden sind. Auch für die Entwicklung des Zellnetzes lassen sich jeweils bei akrokarpen Laubmoosen bzw. bei pleurokarpen übereinstimmende Verhältnisse feststellen. Das Zellnetz aus weiten 5- bis 6-seitigen Zellen (Bryaceen, Mniaceen) nimmt eine Übergangsstellung ein.

Aufgrund dieser Untersuchungen muß die Frage aufgeworfen werden, ob nicht der akrokarpen und der pleurokarpen Wuchsform bzw. dem parenchymatischen und prosenchymatischen Zellnetz mehr systematische Bedeutung zugemessen werden muß, als dies bisher geschah.

H. J. MARESQUELLE (*Institut de Botanique, Strasbourg*)

Exemples tirés de la cécidologie et de la tératologie, pour la théorie d'une information graduelle de la morphogenèse, par des inductions successives et indépendantes

1. Inductions cécidogènes: Les expériences sur la morphogenèse des galles par ablation du parasite à des stades définis (O. Rohfritsch) conduisent à décomposer la cécidogenèse en une série d'étapes, dont chacune s'accomplit par une action spéciale et indispensable du parasite. L'ablation supprime toute induction non encore donnée; mais elle laisse agir les inductions déjà apportées et elle en provoque l'expression au delà de la normale.

2. La morphogenèse normale s'accomplit-elle, elle aussi, par une série d'inductions successives, et indépendantes? On ne peut donner de réponse générale; mais voici quelques exemples où l'on voit un agent extérieur annuler une ou plusieurs déterminations morphogénétiques naturelles, démontrant par là leur existence distincte.

a. Eucécidologie, le parasite, avant d'apporter les inductions proprement cécidiennes, efface tout ou partie des inductions naturelles (vocations d'allongement, de lignification, de développement sexuel etc...).

b. Les virescences florales, provoquées par des actions très variées (virus, mycoplasmes, Acariens cécidogènes, photopériode contraire à la floraison, substances telles que 2–4–d hydrazide maléique...) expriment la suppression de certaines inductions florales, en sorte que s'expriment seules (mais fortement!) les inductions antérieures non enlevées; il en résulte une structure végétative, ou au moins imparfaitement florale. Dans le cas de l'ovule ou résume les faits observés en proposant de présenter comme suit la série des inductions ovulaires.

1. Si la virescence est très profonde, il ne reste de la détermination ovulaire que l'état méristématique initial: celui ci ne peut donner que tige et feuilles (observation très fréquente chez les Saules: "Wirrzöpfe.');

2. Si l'agent de virescence intervient un peu plus tard, le méristème a déjà reçu la vocation de croissance foliacée = isolée, celle ci se fait activement, l'ovule prend l'aspect d'une feuille, porteuse d'un petit massif, qui est le nucelle;

3. En cas de virescence plus tardive, le nucelle a reçu vocation de grandir; et l'organe foliacé qui le porte a reçu mission de s'enrouler en cornet autour de lui;

4. Enfin le dernier stade, celui qui se réalise dans la vie normale (en l'absence de tout effet anti-induction) comprend l'achèvement du nucelle et sa couverture exacte par l'organe foliacé, devenu tégument.

Kl. SCHMIDT (*Botanisches Institut Justus Liebig Universität, Giessen*)

Morphologische und anatomische Untersuchungen an Marsileaceae

Die isolierte systematische Stellung der Marsileaceae zeigt sich an stark abgeleiteten eigenständigen Strukturen, die im Zusammenhang mit der besonderen Lebensweise zu sehen sind. – Bei *Marsilea* sind den einzeln stehenden Blättern je eine Seitenspross- und eine Wurzelanlage zugeordnet. Die Blätter lassen sich von normalen pinnaten Fiederblättern ableiten, sie können sich je nach Umweltbedingungen als Land – oder als Wasserblätter differenzieren. Die Sporokarpien entsprechen fertilen Fiedern, in deren recht komplizierter Entwicklung die Sori infolge Umwachsung und Überwachsung durch marginale Gewebepartien und Indusiengewebe im Inneren des Sporokarps eingeschlossen werden.

M. M. A. SASSEN (*Botanisch laboratorium, Nijmegen*)

Submikroskopische Morphologie des Griffelleitgewebes

Das Leitgewebe des geschlossenen Griffels und das Gewebe, das den Griffelkanal auskleidet, kann man morphologisch und funktionell miteinander vergleichen. Zellen beider Gewebe sezernieren eine Substanz, die sich zwischen den Zellen, beziehungsweise im Griffelkanal, anhäuft. Diese Substanz liefert wahrscheinlich Nahrungsstoffe für den wachsenden Pollenschlauch und kann chemotropisch aktiv sein. Die Interzellularsubstanz darf nicht als Mittellamelle aufgefaßt werden. Die Kollenchymnatur des Leitgewebes hat sich nicht bestätigt.

SASSEN, M. M. A. (1973): *Acta Bot. Neerl.*

M. L. DIJKSTRA (*Botanisch laboratorium, Leiden*)

Light and electron microscopic observations on suberin deposition in wound-cork

Hypocotyls of castor bean seedlings are superficially wounded. Light and electron microscopic observations on wound reactions in cortex cells bordering the wound are made at different intervals after wounding, varying from a few hours to thirty days. After two days, cells near the wound surface start dividing, followed by the formation of a cambium-like structure. At the same time suberization and a slight lignification takes place in cell walls bordering the wound. Later, the outer part of the newly formed cell walls also suberize, but without lignification. Attention is also given to the ontogeny of the suberized layer.

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JOB KUIJT and DAVID R. DOBBINS (*University of Lethbridge, Alberta, Canada, and Wellesley College, Massachusetts, U.S.A.*)

The young primary haustorium of Phthirusa pyrifolia (Loranthaceae)

The radicular disk of *Phthirusa pyrifolia* (Loranthaceae) in the early stages of germination is characterized by a simple internal organization (epidermis, hypodermis, and core parenchyma). This organization evolves into an exceedingly complex one when the disk flattens out against the host surface. The epidermis in the area of host contact is transformed into an intricate layer each cell of which has several branched, thin, tubular downward extentions which entwine with each other and with similar ones of neighboring cells. The tubular portions are enucleate, and have bulbous tips with extremely thin distal walls which appear to rupture, releasing their contents on the host's surface. The core parenchyma of the haustorium contains a striking but as yet unidentified fibrillar material in great quantity. The so-called gland of the haustorium consists of two types of cells, one with light-staining, the other with dark-staining cytoplasm.

A cavity forms at the base of the gland, and fills with a substance optically identical with the above-mentioned fibrillar substance. The gland cavity eventually extends through the contact zone where its contents exude onto the host's surface. The primordial endophyte is initiated above the gland and grows through it to the host surface. Several succeeding penetration attempts may be made before one is successful in entering host tissues.

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POLLEN SYMPOSIUM ON OCTOBER 30, 1971

M. TH. M. WILLEMSE (*Botanisch Laboratorium, Universiteit Nijmegen*)

Ontogeny of pollen

The pollen wall morphology gives for each type of pollen a specific appearance. During on-togeny of pollen many other distinctions could be observed when the changes in the population of cell organelles and some physiological features were considered (LINSKENS, 1969; HESLOP–HARRISON 1971). However, processes occur which could easily be compared in many pollen types: callose wall formation around the developing microspores, the appearance of nucleolar-like bodies in the cytoplasm, the renewal of the ribosome population before the meiotic as well as the mitotic metaphase, and in Gymnosperms the formation of invaginations of the nuclear membrane during the tetrad stage (DICKINSON & BELL 1970; VASIL & ALDRICH 1970; WIL-LEMSE 1971a, 1971b, 1972). Besides, the determination of the pollen wall pattern, a result of the excretion of the content of Golgi vesicles and locally a resisting contact between the plasma membrane and the callose wall, seems to be a more common process in pollen (WILLEMSE 1971c, 1972) and probably in liverwort spores (HORNER, LERSTEN & BOWEN 1966). The ma-terial of the pollen wall, mainly the sporopollenin, originates from the microspore and the tapetal cell.

The relation between the developing microspores and the tapetal cells is partly known. The tapetal cells form callose wall affecting enzymes, the sporopollenin and pigment substances (ECHLIN 1971; WIERMANN & WEINERT 1969). Contact between the microspore and the fluid of the locus by means of thin channels in the intine exists in *Gasteria verrucosa*. In the formation of the pollen wall the haploid nucleus functions in a cytoplasm of diploid origin. The nuclear information is probably given before the total separation of the four microspores in the early tetrad stage.

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SYMPOSIUM ON ECOLOGY ON MARCH 4, 1972

J. J. BARKMAN (*Biologisch Station, Wijster Dr.*)

Some aspects of botanical synecology

The development of synecology has been hampered by the use of concepts both too wide and too narrow from a logical and practical viewpoint. The first definition (Schröter, 1902), "the science of plants that live together", was too wide, including as it did the whole of descriptive plant sociology. Du Rietz' later definition was too narrow, confining this science to the study of environmental factors (mesology) and of the habitat ranges of plant communities and their tolerance of individual factors.

Synecology was more properly defined by Pavillard and Braun-Blanquet. It centers around the question: how does a plant community fit into its habitat by its structure and its performance (functioning) and how does it maintain itself against adverse factors? Two highly complex notions are included in this problem: "habitat" and "plant community". The concept of habitat varies with its object and is different for a leaf, a whole single plant, a plant population, a synusia, a plant community, a biocoenosis, and an ecosystem. It is also quite different – in exactly the same locality – for a soil fungus, a lichen, an annual herb, and a tree.

Population ecology deals with populations of single species, synecology with communities, i.e. plant assemblages that consist – in principle – of many species. So-called monospecific communities like the *Salicornietum herbaceae* are not monospecific at all, if bacteria, algae, fungi, lichens, and bryophytes are also taken into consideration, as should be done. The study of such communities does belong to synecology, not, however, the study of plant assemblages without a natural arrangement (flower beds) or without interrelations between the individuals (open, initial stages of vegetation on bare soil).

Synecology does not necessarily deal with clear-cut communities only, it can also deal with ecoclines, as is done in recent work on gradient analysis. The variation in habitat along gradients can be studied and correlated both with the sequence of species, life form groups, ecological groups, and community types, also with such abstract notions as the variation of species diversity.

At present it looks as if we have a fair knowledge concerning the range of the principal physical and chemical factors in certain plant communities, at least as far as flowering plant communities in Europe are concerned (cf. Ellenberg, Vegetation Mitteleuropas). However, the gaps are numerous. Very little is known about the influence of trace elements in natural vegetation. Yet, lithium, for instance, appears to play a very important rôle. Even cation exchange capacity and nitrification rate of natural soils are often unknown. As to microclimate, much work has to be done on the spectral composition of the light in the vegetation and on saturation deficit of the air close to the soil surface. Even the temperature of the soil surface is often not measured correctly.

Actual concentrations of an element in the soil may be misleading, because most of it may be concentrated in the living plants or in the litter. Recent investigations also tend to show that proportions between factors and the rate of fluctuation of a factor in time (even within 24 hours) are more important with regard to plant distribution than momentary measurements of absolute concentrations. Spatial variation can be enormous even within a single community stand, so that many measurements of the same factor are needed both in time and in space.

Other complications arise when the vegetation pattern is interpreted in terms of habitat pattern. It is often difficult to decide which factors are limiting. Also, correlations may be non-causal, because of a close correlation between the investigated factor and the decisive factor. Nitrification rate and soil phosphorus content, for instance, are often closely correlated, being both dependent on a third factor, and many so-called nitrophilous plant communities actually seem to be merely phosphatophilous. Some factors only affect vegetation through others. The problem of "chalk loving " and "silicate loving" plants is a most illustrative example. With progress of research emphasis has shifted successively from cretaceous (the geological formation) via calcium carbonate, carbonate, pH, and soil texture to microbial soil activity and

finally to the amounts of available phosphorous and nitrogen as factors affecting vegetation.

Causal synecology is further complicated by the fact that vegetation and habitat influence each other (so what causes what?) and by the fact that the tolerance of a plant community for one factor is affected by the intensity of almost any other factor. Consequently, there is a marked shift in habitat of communities from one climatic region to another. Needless to say that the geographical distribution (macropattern) of vegetation is also determined by historical factors and accessibility.

Many communities probably occupy non-optimal compromise habitats, either because 1° the ideal combination of factors is physically or chemically impossible in nature (sometimes possible in a phytotron), or 2° because it does not occur in the area (or part of the area) of the community, or 3° the community is excluded from that habitat by competition. Even if habitat is optimal for the community, it need not be so for each species, as different species hardly ever have identical requirements.

It is therefore not surprising that a full causal analysis has not yet been carried out for any plant community so far. It is even questionable whether this is possible. In view of the many correlations, interrelations and interferences both between habitat factors and between the individuals and species of a plant community, as well as between the one set of variables and the other, experimental work (isolation of factors) is indispensable. Every experiment means a sudden change in environmental conditions. We cannot separate the effect of the new value of the changed habitat factor from the simultaneous effect of the change itself. Every intervention disturbs the community, makes it more homogeneous and poorer in species. It favours the establishment of disturbance indicators alien to the community. They are often fast growing species indifferent to many habitat factors.

Therefore experiments carried out so far have mainly dealt with plant communities that are already homogeneous, poor in species, often short-lived and adapted to great fluctuations in environmental factors, such as pioneer communities, grass lands and weed communities in arable land, or even artificial mixtures of a few cultivated plants. This explains why experimental synecologists (and most autecologists, for that matter) regard competition as the principal or even sole form of interplay between plants.

Competition is stronger as the demands of the plant individuals for water, minerals and light per time unit are greater, and this is the very case in fast growing species. Competition is also stronger the more the plants have the same environmental requirements, i.e. in populations of one or communities of a few species only, which is the case in the experiments. It was found that simulation models for ecosystems fail (because the mathematical treatment becomes too complicated), when more than ten species are involved. And these are simplified models in which competition is assumed to be the only kind of interplay!

Other kinds of relations than competition occur where humus is present (saprophytes, mycorrhiza), where stable communities are formed (mutualism, symbiosis), where plants of very different size, growth-form, life-form and duration of life occur side by side (leading to phenomena like priority, protection, epiphytism, climbers and lianas).

Like competition, parasitism and allelopathy, too, have been overestimated. It is pointed out that parasitism has better chances in unstable communities and in monocultures, allelopathy in pioneer communities because humus tends to neutralize most of the growth promoting and inhibiting substances excreted by roots. Arable fields are to be considered plant communities that are kept constantly in a pioneer stage. They are monocultures, unstable (unless man interferes which he does) and have a mineral soil poor in humus. In this biotope competition, allelopathy, and parasitism are the only plant interrelations of significance, with competition as the dominant factor.

In a climax forest, on the other hand, many forms of interplay occur in addition to competition, whereas parasitism and allelopathy are negligible factors. Even cultivated woods, although having a fairly complicated structure, are distinctly poorer than natural forests, having significantly less epiphytes and lianas or none at all.

There are other fundamental differences between advanced, natural communities, especially primeval forests, and cultural communities, particularly fields. The former are much more stable, richer in species, in variety of taxonomic groups of plants and animals, in growth and

lifeforms, pollination and dissemination types, in biochemical diversity. Their members have a longer duration of life, lower growth rate, lower natality and lower mortality than those of cultures, and they have more efficient means of dispersal. In short, they live much more economically. Their culm/root ratio is also much lower. Fewer nutrients are present in the soil and many more in the standing crop. Productivity and energy flow are smaller than in arable land, but their biomass is much greater. The energy flow passes through many more trophic levels. The influence of the vegetation on the environment (soil, microclimate) is much greater and so is therefore their independence from that environment. Their economy is more closed. There is more recycling and a smaller amount of nutrients leaves the system.

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Competitive studies based on mono- and bicultures

In studying interactions between plant species, biologists generally observe individual plants and investigate how populations are controlled, whereas agronomists observe entire crops and prefer parameters based on area units. Why this different approach?

Biologists are more concerned with vegetations and agronomists with sown annual crops. These two subjects differ essentially in at least three aspects:
1. In a vegetation the environment greatly determines the species composition, which is a very long-term process from generation to generation and results in a more or less stable association. In arable land, however, man frequently selects the species for just one year. Within short periods great changes in botanical composition may occur, often leading to dominance of one species.
2. Compared with nature with its complicated biotic and abiotic structure, in cultivated land soil and crop are much more homogenized. It may be assumed that in a heterogeneous environment interactions between plants are less intensive, since the species grow and multiply in their own microsites which are better adapted to their specific requirements.
3. A cultivated crop usually has a much higher production level than a vegetation, because the former can be supplied with minerals *ad libitum*. In cultivated land encroachment will be more intensive, competition for space being, therefore, of great importance.

For these reasons competition is often less fierce in a vegetation than in a cultivated crop and biologists persist in thinking, therefore, in terms of the performance of individual plants instead of space, space being defined by that part of the environment explored by a species (DE WIT 1960).

In measuring competition a species' performance in one situation is compared with that of the same species in another situation and with the performance of other species. By taking above-ground yields, it is obvious that 10 g dry matter of a grass is not equivalent to 10 gr dry matter of an herb and not equivalent to 10 gr dry matter of the same grass species but grown in a different period of the year. This difficulty can be met by referring to some standard permitting a dimensionless measure to be calculated. This can be done by comparing the performance of the species on the basis of relative yields, defined by $r = O/M$, in which O is the yield of a species per area unit in mixture and M the yield of the same species in monoculture, grown under the same conditions except for the interspecific competition.

This procedure is justified, because species in a mixture often crowd for the same space, i.e. the sum of the relative yields of the species or the relative yield total (RYT) equals 1 (VAN DEN BERGH 1968).

This is shown by experiments designed according to the replacement principle. By definition the sum of the relative seed or planting frequencies in these experiments equals 1. The relative seed or planting frequency of a species is the quotient of the seed or plant number in the mixture and that in pure stand.

The various ways of competition may be distinguished by their RYT values.

Model I. RYT = 1. The species crowd for the same space and one species will dominate in due time (VAN DEN BERGH & ELBERSE 1970; GIGON 1971).

Model II. RYT >1. One or both species are less affected than might be expected from crowding for the same space and a stable equilibrium may establish (ENNIK 1970).

Model III. RYT <1. One or both species are more affected than might be expected from crowding for the same space and an unstable equilibrium may establish (SANDFAER 1970).

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Plant physiology and ecology

Theoretically there is little doubt as to the significance of plant physiology for applied sciences like agriculture, horticulture and forestry and the same holds for ecology since in all circumstances it is the individual that responds to changes in the environment. Practically, however, there is considerably more doubt since many plant physiological studies often give the impression that plant physiologists have lost their interest in one of the original aims of plant physiology as expressed by Pfeffer, "die Physiologie hat die Aufgabe die Vorgänge im lebenden Organismus nach Mass und Zahl festzustellen, auf ihre Ursachen zurückzuführen und in ihrer Bedeutung für den Organismus kennenzulernen", and it is the latter that counts for ecologists and agriculturists. The present state of affairs is a consequence of the other aim of plant physiology, "die Vorgänge nach Mass und Zahl festzustellen", which has attracted the more research workers as more and better equipment became available. The preponderance of attention paid to the lower levels of organization in the sequence: subcellular structures, cells, tissues, organs, organisms, populations, communities, ecosystems, and biosphere has greatly enlarged the gap between plant physiology and ecology and this has already led to the situation that details obtained do not contribute sufficiently to an understanding of their significance in the functioning of the organism. Hence this complaint does not only concern ecologists but as well "whole plant" physiologists, and in our planning we should consider an even development of all organization levels and should not unevenly focus our attention on the lower end as a consequence of our wish to reveal the last detail, nor on the upper end in our concern with landscape and pollution.

Notwithstanding these general trends there are and always will be plant physiologists who are interested in integration of detailed knowledge in order to understand the reactions of individuals to the environment, and their possible contribution to ecology should not be underestimated by ecologists as much as has been done in the past. When we tentatively assume that the descriptive approach of ecology used so far has yielded all obtainable information and that it has proceeded from that information to causal conclusions, ecologists and plant physiologists may march on together to test these hypotheses experimentally. I feel ecologists could benefit more from plant physiological procedures in attacking their problems.

A number of examples may serve to demonstrate this approach with regard to an analysis of the effects of environmental factors on leaf area development, one of the aspects with a certain importance for survival of plants in competition with others.

1. *Light intensity* affects plant growth in many ways. The dependance of photosynthesis on light intensity can be demonstrated by the well-known saturation curve. Since the saturation level can be changed by enhancement of the CO_2-concentration and/or the ambient temperature the process of photosynthesis can be used successfully for demonstrating the phenomenon of limiting factors which, in turn, depending on the level of the others, determine the course of the curve. Although the general responses are rather similar for all plants in the last decades we have learned that both the saturation level and the response to temperature may show species differences and even differences between varieties. But even more interesting than these genetically controlled differences are those due to variations in the light climate during growth as e.g. sun and shade leaves and sun and shade plants where not only the adaptation of leaf morphology and leaf anatomy determine the photosynthetic capacity per unit leaf area but where the whole plant structure is adapted in such a way that the highest benefit can be obtained from the prevailing light intensity.

2. *Soil moisture potential* affects leaf area development through the influence on plant water potential. Here again the relation between leaf water potential and soil water potential is complicated by other factors. High transpiration conditions, like high light intensities and low air humidities, increase the unfavourable effect of low soil water potentials. On the other hand, morphological adaptations in leaf structure and leaf/root-ratios tend to reduce this effect and are essential for survival.

3. *Gas exchange* properties of soils may differ considerably depending on soil structure and soil water content. Insufficient gas exchange leads to a reduced oxygen supply to the root surfaces and enhanced carbon dioxide concentrations. The concomitant reduction in root growth results in a lower absorption rate of water and minerals. Hence leaf area development is hampered and interactions with transpiration conditions and soil mineral content accentuate or alleviate the ultimate response. As in the two examples mentioned above, plants differ in sensitivity but are also able to adapt by the formation of air channels in the root cortex which are connected with the ambient air via the intercellularies in the above ground parts.

In addition to differences in sensitivity and adaptability plant reactions also depend on their stage of development. This is partly because during growth plants change their own environment resulting in changes comparable to those accompanying ambient conditions. Besides, during plant life there is a gradual change in the nature of processes limiting plant performance, from mobilization of reserves in the early stages through water and mineral absorption for optimal leaf development to leaf area duration for building up the reserves for the next generation.

The complexity, already clear from these few examples, demonstrates that if ecological research should benefit from physiological experience, the ecologist and the physiologist should work side by side. The experience with such a combined approach obtained in agricultural research guarantees useful results. Since technical equipment already is or will be available in the near future for measuring and registering many physiological processes under field conditions periodically and perhaps even hourly, limiting factors can be traced. In addition it stands to reason that, as in agriculture, computers will be helpful for quantifying effects over longer periods.

MEETING OF THE SECTION FOR PLANT PHYSIOLOGY ON MARCH 10, 1972

G. A. Pieters (*Afdeling Plantenfysiologisch Onderzoek, Wageningen*)

The growth of leaves of Populus euramericana 'Robusta' in relation to light intensity, temperature, age, and root environment

The demands of plants on water and ion supply increase with light intensity, temperature, and age. Consequently interactions of growth and root environment should be taken into account when studying the relation of growth to irradiation level, temperature, and age When the root environment is inadequate, the (apparent) relation between irradiation level and growth rate often shows an optimum, which can be shifted to higher light intensities or even disappear when the conditions in the root environment are improved or become optimal. Only then the specific effects of irradiation level, temperature, and age on growth can be studied.

In "optimally" growing poplars the increasing length and width of the individual leaves in the linear phase of growth possess a linear relationship to each other, according to Width $=$ Length -2 (in cm). This relationship appears not to be affected by irradiation level, temperature, and age. The growth rate of the leaves in the linear phase of growth does not depend directly on irradiation level, but on temperature and is proportional to final leaf size. Since in mature leaves mean epidermal cell size is independent of irradiation level, temperature, and age of the plant, cell number is the main determinant of leaf size and of linear growth rate. Hence it should be concluded that the growth rate of the individual epidermal cells is little dependent of irradiation level, age of the plant and ultimate size of the leaf, but temperature influences it. Obviously the time needed for the development and maturation of a leaf is constant at constant temperature.

In high and low light intensity small plants produce small leaves. Mature leaf size increases with leaf number at a rate independent of irradiation level or temperature. The same holds for linear growth rate, because of the correlation between both. Notwithstanding this increasing growth rate with leaf number, the difference in length of successive leaves remains constant. Evidently, this implies that leaf initiation rate and growth rate are closely correlated and are both proportional to mature leaf size. Because of their constant difference in length, the lengths of the succession of leaves can be described as a descending arithmetical progression. On this basis the total leaf area growth of the plant can be calculated and expressed in the length of the youngest mature leaf, L, as $\triangle$ Area/unit time $\simeq CL^3$, in which C is a temperature-dependent constant.

The increase of the size of successive leaves comes sooner or later to an end: maximum mature leaf size is related to irradiation level according to $L_{max} \simeq f(\sqrt[3]{Irr.})$.

This indicates that in young plants leaf growth is not limited by carbohydrate supply and that leaf size increases until total leaf area growth ($\sim L^3$) is in equilibrium with supply or with irradiation level.

J. ROMBACH (*Afdeling Plantenfysiologisch Onderzoek, Wageningen*)

Two modes of growth stimulation by light in Lemna minor L.

The multiplication rate of *Lemna minor* in axenic culture on a nutrient medium with 1.5% sucrose and 0.026% casein hydrolysate decreased after transfer from light to darkness until a low level had been reached (ROMBACH 1971).

After a 7-day-period of darkness a brief illumination (5 minutes red light of 6000 ergs/cm² sec) gave a temporary growth stimulation. Since the effect of red light was nullified if a treatment with far red followed the red illumination, this effect was considered to be due to phytochrome in the far red absorbing form acting during the period of darkness after the red illumination (ROMBACH 1971, FRICK & MOHR 1973).

The growth stimulating effect of repeated brief illuminations with red light was only partly reversible by far red given after each red exposure. The shorter the dark periods between the light exposures, the higher the resulting growth rate, but such part of the effect as could be reversed by the far red treatment (the phytochrome effect) did not increase. Far red itself had no growth stimulating effect but kinetin further increased the irreversible part of the light effect.

It was concluded that the growth stimulation by brief illuminations was due to 1° the phytochrome photoconversion and the subsequent action of phytochrome P_{fr} in darkness and 2° a different effect of light.

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MEETING OF THE SECTION FOR PLANT PHYSIOLOGY ON SEPTEMBER 8, 1972

C. KOLLÖFFEL* and G. A. KAMERBEEK** (*Botanisch Laboratorium, Utrecht en **Laboratorium voor Bloembollenonderzoek, Lisse)

Respiratory activity in Iris bulbs after a cold treatment

Newly lifted Iris bulbs are in practice often stored at 30 °C to retard vegetative growth. When transferred to 13 °C they start growing again. The present study deals with the respiration rate and the mitochondrial activity of Iris bulbs (*Iris hollandica* cv. Wedgwood) stored for 6 to 8 months at 30 °C ("retarded bulbs") and subsequently subjected to a temperature treatment of 13 °C during 1 to 3 weeks.

Oxygen consumption was measured by Warburg manometry. Homogenates of the bulbs were differentially centrifuged twice, in order to obtain fractions enriched with mitochondria. Mitochondrial activity was determined by measuring polarographically the oxidation of succinate and the corresponding respiratory control ratio (RC) and ADP to O ratio. The bulbs were divided into (a) the scales, (b) the base-disc without the socle and (c) the central "bud" including the growing point and the sheath leaves.

In accordance with earlier observations RODRIGUES PEREIRA 1962. KAMERBEEK 1962) it was found that the respiration rate of the retarded bulbs was low (6.7 μmoles O_2/hour/bulb), but increased within 3 weeks storage at 13 °C to about 30 μmoles O_2 consumed per hour per bulb. Besides it was found that the increase in the respiration rate of the whole bulb may be largely attributed to an increase in the respiration rate of the scales.

Mitochondria from all three parts of the retarded bulbs showed a reasonable respiratory control. After transition to 13 °C the RC ratio (2.0 to 3.0) and ADP/O ratio (0.9 to 1.3) hardly changed, indicating that the phosphorylation efficiency and the integrity of mitochondria from bulbs at a low metabolic activity are nearly the same as those from bulbs with an activated metabolism. The activity of the mitochondrial succinate-oxidase system from the base-discs increased (0.016 to 0.025 μmoles O_2/min/base-disc) and also that from the buds increased (0.012 to 0.104 μmoles O_2/min/bud) after transition to 13 °C. Concurrently, the in vivo respiration rate of these two parts nearly doubled. The increase in the in vivo respiration rate of the scales was, however, not accompanied by an increase in their mitochondrial succinate-oxidase activity (0.25 μmoles O_2/min/scale).

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MEETING OF THE SECTION FOR VEGETATION RESEARCH ON
DECEMBER 19, 1972

A. J. DEN HELD (*Hugo de Vries-laboratorium afd. Vegetatiekunde, Amsterdam*)

A comparative study of the vegetation and flora of recently formed peat areas
in the fens in the western part of the Netherlands*

The fens investigated have the common feature of being former peat exploitation areas in those
peat-carrying zones of the Western Netherlands with carr peat, which lay above the sediments
of the Calais transgression. In the large ditches and parts of the broads formed by peat dredging
new land has been formed, the so-called "kragge". This consists of a more or less floating, c.
0.2–0.8 m thick peat layer fixed at one or more sides to the remnants of the original peat.
Most new land has been formed in the last 50–200 years. The Ilperveld (province of Noord-
Holland), the Botshol (prov. of Utrecht), and the Nieuwkoopse Plassen (prov. of Zuid-
Holland) are the main fens investigated. The main factor influencing the vegetation and the
flora seems to be the salinity of the open water (and perhaps some properties coherent with it).
At present the salinity in the Ilperveld is about 600–750, in the Botshol about 600–900, and in
Nieuwkoop about 170–300 mg chlorine/l. The Ilperveld, however, has been much more
brackish (mesohalinic) in the past, just like the Wormer-Jisperveld north of it, which is now
nearly fresh.
  Roughly spoken four vegetation zones can be distinguished on the recently formed peat (note
that this zonation does not necessarily reflect the local succession series):
1. a very wet zone near the waterside, mostly below waterlevel; vegetation poor in species,
   consisting mainly of large helophytes, without mosses (syntaxa: mainly Phragmitetea);
2. a rather wet zone at about water-level; vegetation rich in (often large) forbs, pleurocarpous
   mosses, and liverworts (syntaxa: elements of Phragmitetea, Caricion davallianae, Filipen-
   dulion, Calthion palustris);
3. a still rather wet zone with initial sphagnum-reed vegetation; likewise rich in forbs, with
   relatively many sphagnum species (syntaxa: Caricion curto-nigrae, also elements of those
   of zone 2);
4. a moist zone (water-table about 0.05–0.2 m below the surface) with sphagnum-reed vegeta-
   tion, rather rich to very poor in species; sometimes with some heather species; besides
   sphagnums, often many acrocarpous mosses (syntaxa: Caricion curto-nigrae, Oxycocco-
   Sphagnetea, some elements of the Cirsio-Molinietum).
The marsh woods and shrubberies have not been taken into consideration.
  Several physical and chemical properties of the environment have been measured, i.a. the
spatial variation of the pH and the e.c.c. (electric conductivity capicity) of the ground-water.
These have been measured at three levels (at the surface and at 0.4 and 0.8 m below it). In the
first zone the pH and the e.c.c. are about the same at the various levels. More inland they de-
crease strongly at the surface; at 0.4 and 0.8 m this decrease is much less strong, except for a
great decline of the e.c.c. in many places in Nieuwkoop. So the subsoil is less acid and mostly
much richer in electrolytes than is the surface. Periodical measurements of the water-table
show it to fluctuate more or less (a few cm to 1 dm at most) in all "kraggen".
  In the table the numbers of geographically differential species for the different fens are
shown. In the Ilperveld the high presence and abundance in some zones of *Hydrocotyle vul-
garis, Scirpus lacustris* ssp. *glaucus*, several fern species, and *Drepanocladus fluitans* are
striking. In the Botshol and Nieuwkoop the rich growth of thalloid liverworts (in particular
Pellia neesiana) in zones 2 and 3 is conspicuous, as is the common occurrence of scattered
shrubs. Characteristic and common plants in the Botshol are *Cladium mariscus* (zone 1) and
Carex curta (zone 4); in this area hardly any heath species occur. In Nieuwkoop *Molinia
caerulea* is very abundant in the sphagnum-reed vegetations. The different vegetation units are

on the whole richer in species in the Botshol and especially in Nieuwkoop than they are in the Ilperveld.

The Wormer-Jisperveld, which is now nearly fresh, has a vegetation that strongly resembles that of the Ilperveld.

Special attention has been paid to the pattern of rooting of a number of the plant species concerned. The investigation of root systems supplements the description of the vegetation and gives more insight in the composition and the origin of the vegetation. The following statements can be made:

a. A number of species with their optimum in zone 1, but penetrating less vitally into zones 3 or 4, are literally waterside relicts, as is shown by the older parts of their root system (e.g. *Thelypteris palustris, Rumex hydrolapathum, Cladium mariscus, Potentilla palustris*).

b. Characteristic waterside species that also occur in all types of sphagnum-reed vegetation reach with their roots deeply to very deeply (0.3 to c. 1 m) everywhere (*Phragmites australis, Scirpus lacustris* ssp. *glaucus, Juncus subnodulosus*).

Table. *Numbers of geographically differential species.* The numbers in bold type relate to very distinct differential species, the other ones to weaker differential species.

	Ilperveld		Botshol		Nieuwkoop	Ilperveld
zones 1 and 2	6,8	**4,2**	1,1	**26,9**	7,7	
zones 3 and 4 (parts rich in species)	7,8	**2,3**	2,1	**20,9**	9,5	**1**
zone 4 (parts poor in species)	4,2	**1**	1	**5,1**	7,4	**4,1**

c. Some deep-rooting waterside species disappear already in zones 2 or 3. They tend to develop a more superficial root system – consequently in a more acid environment – in the inland zones (*Typha angustifolia, Iris pseudacorus, Carex paniculata, Cladium mariscus*).

d. Many species mainly restricted to zone 1, 2, or 3, respectively, root superficially (to a depth of 0.05–0.1 m at most); i.a. *Atriplex* sp. and *Solanum dulcamara* in zone 1; *Valeriana officinalis, Eupatorium cannabinum, Lychnis flos-cuculi*, and *Liparis loeselii* in zone 2, sometimes also in zone 3; *Succisa pratensis* and *Hammarbya paludosa* in zone 3. Species rooting slightly more deeply, like e.g. *Peucedanum palustre* with its optimum in zone 2 and 3, penetrate farther into the sphagnum-reed vegetation.

e. Some moderately to strongly acidophilic species occurring in several zones, however, appear to root very superficially; they are favoured by the superficially beginning acidification (*Drosera rotundifolia, Potentilla erecta*).

f. Some more or less strongly acidophilic plants occurring only in the parts of zone 4 with a low pH and e.c.c. root rather deeply to deeply (to a depth of about 0.15–0.35 m), i.a. *Molinia caerulea, Eriophorum angustifolium, Erica tetralix, Vaccinium vitis-idaea*. Deep-rooting species characteristic for the less acid and poor parts of zone 4 are, i.a., *Carex curta, Juncus subuliflorus*, and *Dryopteris cristata*.

g. *Hydrocotyle vulgaris, Agrostis canina*, and *Anthoxanthum odoratum* root superficially but show a very wide ecological amplitude.