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The Physiotype Concept – an Approach Integrating Plant Ecophysiology and Systematics

By

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Summary

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Several attempts have been made to arrange plants in certain groups according to their physiological properties. Whereas chemotaxonomy placed emphasis on so-called “secondary metabolites” to improve our knowledge on natural systematic relationships on different hierarchy levels, “the physiotype concept” of KINZEL 1972, 1982 and ALBERT & KINZEL 1973 strongly incorporates ecological aspects. According to this concept, the term “physiotype” refers to a certain taxonomic unit (species, genus, family etc.) with common physiological features, which enable it to cope successfully with specific ecological situations. Originally, the “physiotype-concept” focused mainly on mineral ion and organic acid metabolism and soluble carbohydrate patterns. However, towards an overall understanding of the ecological behaviour of a taxon, as many physiological attributes as possible must be taken into account. According to new findings in the fields of plant ecophysiology, stress physiology and biochemical ecology, the physiotype concept must also consider the occurrence of low molecular weight compounds acting as cytoplasmic osmolytes (compatible solutes), and bioactive natural compounds. This holds true also with regard to attributes of the nitrogen metabolism, particularly the preferential form of inorganic nitrogen uptake. Furthermore, to characterize a certain plant taxon in a holistic approach, the combination of physiological and biochemical with morphological and anatomical features has to be considered.

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Zusammenfassung

CHOO Y.-S. & ALBERT R. 1997. Das Physiotypenkonzept – Ein Ansatz zur Integration von Ökophysiologie und Systematik der Pflanzen. – *Phyton* (Horn, Austria) 37 (1): 93–106. – Englisch mit deutscher Zusammenfassung.

Der Versuch, physiologische Eigenschaften von Pflanzen zu ihrer Klassifikation mit heranzuziehen, ist wiederholt unternommen worden. Während die Chemotaxonomie im wesentlichen auf sogenannte „sekundäre Inhaltsstoffe“ zurückgreift, um unsere Kenntnisse über natürliche Verwandtschaftsverhältnisse zu vertiefen, schließt das „Physiotypen-Konzept“ von KINZEL 1972, 1982, sowie von ALBERT & KINZEL 1973 ganz gezielt auch ökologische Aspekte mit ein. Demnach ist ein „Physiotypus“ eine bestimmte taxonomische Einheit (Art, Gattung, Familie, . . .) mit einem gemeinsamen Muster spezieller physiologischer Merkmale, das die Voraussetzung für die erfolgreiche Auseinandersetzung dieses Taxons mit spezifischen ökologischen Situationen ist. In der ursprünglichen Fassung konzentrierte sich das „Physiotypen-Konzept“ hauptsächlich auf den Mineralstoffwechsel und den Haushalt von organischen Säuren und löslichen Kohlenhydraten; um das ökologische Verhalten eines Taxons jedoch möglichst umfassend zu verstehen, ist die Kenntnis einer möglichst vollständigen Palette physiologischer Merkmale anzustreben. Entsprechend unserem erweiterten Wissen auf den Gebieten der Ökophysiologie, Streßphysiologie und der biochemischen Ökologie sollten jedenfalls auch niedermolekulare cytoplasmatische Osmotika (kompatible Substanzen) sowie bioaktive Naturstoffe im Physiotypen-Konzept Mitberücksichtigung finden. Dies hat auch für Attribute des Stickstoffwechsels zu gelten, insbesondere für die Charakteristik von Aufnahme und Metabolisierung anorganischen Stickstoffs. Im Sinne eines ganzheitlichen Zuganges zum Verständnis der Ökologie eines Taxons ist schließlich die synthetische Betrachtung physiologisch-biochemischer und anatomisch-morphologischer Merkmale unerlässlich.

Introduction and Historical Dimension

Botanical systematics and plant taxonomy are the sciences of delimiting, describing and naming of any group of plants considered to represent a distinct related unit (taxon) and of arranging all recognised taxa in classification systems. Besides the traditional conception to classify plant taxa by their morphological and anatomical characteristics, mainly of reproductive organs, there have been several attempts to arrange plants in certain groups according to their physiological properties.

Since the pioneer studies of STOCKER and WALTER in the first half of the 20th century, ecology has increasingly made use of physiological methods, and in turn physiology has also frequently considered more and more ecological aspects. A central objective of plant ecology is to understand the causes of plant adaptation and distribution patterns. Many ecologists have approached this goal by studying how various morphological and physiological properties permit a plant to survive and compete successfully in certain environments. Ecophysiology thus provides an im-

portant window to the central mechanisms that underlie species distribution and habitat-specific competitive ability.

Although early attempts (SCHIMPER 1898, STOCKER 1928, WALTER 1936, 1968, 1973) were made to combine ecological behaviour and physiological aspects, plant ecophysiology was first reviewed as a separate discipline by BILLINGS 1957. It is noteworthy that the main emphasis during the early period of ecophysiological research was placed on water balance, osmotic relations – occasionally extended to ion analyses – and gas exchange. The many new findings during that time have accelerated the firm establishment of physiological plant ecology (LARCHER 1973, 1994, KREEB 1974, BANNISTER 1976, ETHERINGTON 1978).

The discovery of the C_4 pathway of photosynthesis (KORTSCHAK & al. 1965) led to great efforts to determine the adaptive significance of this pathway and of its influences on plant distribution. This research also stimulated investigations on the ecology and physiology of CAM plants. Clear relations could be found between climatic conditions, both on a small scale (e.g. within tropical forests) and on a broad scale (vertical and latitudinal gradients), and the occurrence of different types of CO_2 gas exchange (KLUGE & TING 1978, OSMOND & al. 1982, COLLINS & JONES 1985, BENZING 1990, BATANOUNY & al. 1991).

Several models have been developed to explain how plants manage their water and light resources to optimize carbon intake and to maintain growth, including under unfavourable conditions (NOBEL 1991). These theories stimulated new research including aspects of nitrogen metabolism and mineral nutrition of plants as well as the economics of storage of ions and organic compounds (RORISON 1969, CHAPIN 1980, 1988, EVANS 1989, CHAPIN & al. 1990, MOONEY & al. 1991).

For a long time, obviously for economic purposes, the discipline of plant nutrition (originally developed as branches of agronomy and chemistry) had predominantly been applied to crops, with a relative small number of species being the focus of interest. However, as realised from pioneer works (e.g. ILJIN 1936, COLLANDER 1941), connecting phenomena of mineral metabolism and ion uptake processes with ecological questions proved to be rewarding (KINZEL 1982, MARSCHNER 1995)

Consequently, BAUMEISTER & ERNST 1978, ALBERT 1982, KINZEL 1982, 1983, 1984, KINZEL & BERGER 1992, KINZEL & LECHNER 1992, MARSCHNER 1995 and others provided information about special characteristics on the level of mineral metabolism and focused attention on their ecological significance (key words: limestone and silicate plants, halophytes, heavy metal and serpentine plants). Differences in mineral metabolism have been found between higher taxonomic units, e.g. families (KINZEL 1984, 1989), as well as between subtaxa of the same species (EPSTEIN & JEFFERIES 1964, EL BASSAM & al. 1990). In particular, it is worth noting that some distinct

taxa, especially families, are characterized by a typical ionic pattern. In addition to mineral elements, numerous data on low molecular weight organic compounds have been provided recently, showing taxonomical perspectives as well as clear relations to the ecological behaviour and tolerance mechanisms in extreme habitats, particularly under conditions of decreased internal water potential. For example, taxon characteristics were found in halophytes and xerophytes as well as in plants exposed to artificial salt and drought stress with regard to constituents known to act as compatible solutes within the cytoplasm (cytoplasmic osmotica) like amino acids (especially proline), betaines (esp. glycinebetaine), hexitols (esp. sorbitol), and cyclitols (esp. pinitol) (refer to STOREY & al. 1977, STEWART & HANSON 1980, GORHAM & al. 1981, ALBERT 1982, POPP 1984, POPP & al. 1984, GOLAN-GOLDHIRSH & al. 1989, KÄSTENBAUER 1992, HERTENBERGER 1993, PFUNDNER 1993). The crucial role of these organic solutes in improving the ability of plants to cope successfully with adverse environmental conditions becomes more and more evident (e.g. WYN JONES & GORHAM 1983, JONES & al. 1989, SMIRNOFF 1995).

On the other hand, chemotaxonomy (chemosystematics) which initially emphasized mainly so-called "secondary metabolites" (MOLISCH 1933, HEGNAUER 1962–1994) offered tools to improve our knowledge on systematic relationships on a rather low hierarchic level, e.g. subspecies, species or genus. In detail, the use of secondary compounds has clear advantages over the use of primary compounds for studying taxonomic and systematic relationships: whereas the former show qualitative patterns, differences of primary compounds are mostly quantitative ones, and these are subjected to both environmental and genetic control. The existence of common patterns of secondary compounds may provide much clearer evidence of natural relationships than morphological similarities. The probability of the convergent evolution of whole clusters of compounds ("fingerprints") seems to be lower than on the less complex morphological level. Thus, chemotaxonomical research proved to be very successful (refer to SEIGLER 1977, HARBORNE & TURNER 1984, HEGNAUER 1986, WATERMAN & GRAY 1987). However, it is clear that the different groups of secondary compounds are not equally valuable in tracing relationships at all taxonomic levels and the choice of appropriate secondary compounds is of paramount importance when undertaking chemotaxonomical studies. In addition, there is growing interest in biochemical and ecological aspects of these compounds: a) in essential links to the primary metabolism (e.g. carotenoid, steroid, flavonoid, alkaloid, etc.), b) in their possible function as storage of carbon and essential nutrient elements, esp. N, P, S, c) as root exudates, d) as protective agents and chemical signals in the ecosystem, e) for allelopathic effects and f) as phytoalexins (LEVIN 1976, SEIGLER 1977, SWAN 1977, SCHLEE 1986, MARSCHNER 1995). Therefore, the term "second-

ary compounds" should better be replaced by the term "biologically active compounds" (SCHLEE 1986). Recently, these items of "biochemical ecology" or "ecological biochemistry" have been illustrated in many publications (LUCKNER & al. 1976, SCHLEE 1986, HARBORNE 1978, 1993).

In summary, it is generally accepted that a causal interpretation of the ecological responses of each plant species and/or sometimes higher taxonomic units necessitates the understanding of physiological traits. This has been exemplified for different levels of metabolism (e.g. OSMOND & al. 1980, KINZEL 1982, LANGE & al. 1983, CHABOT & MOONEY 1985, CRAWFORD 1989, SMIRNOFF 1995).

The Physiotype Concept

This concept proposes an alternative approach to classical ecophysiological conceptions: special physiological characteristics are not the consequence of ecological status but rather the genetically fixed precondition for successful environmental adaptations. In the early 1970's, ALBERT & KINZEL 1973 introduced the term "physiotype" in order to describe the physiological peculiarities of a certain taxon (a genus, a family, etc.; KINZEL 1972, ALBERT & KINZEL 1973, KINZEL 1982) – in addition to the morphological characterisation of plant taxa. The central point is that a characteristic physiological pattern of a certain taxon determines or influences its ecological position considerably. Thus, special chemophysiological peculiarities are to be interpreted as essential prerequisites to cope with specific ecological situations, and of course, become more evident through natural selection processes.

Plant Taxa with Prominent Physiological Attributes

To date, the physiotype concept as briefly outlined above has been developed from experimental findings on relatively few plant families with certain typical physiological traits that have been documented by many research groups. Special mineral metabolism characteristics and solute patterns that are at least partially responsible for ecological success or overcoming stress have been demonstrated in the families *Aizoaceae*, *Amaranthaceae*, *Brassicaceae*, *Caryophyllaceae*, *Chenopodiaceae*, *Crassulaceae*, *Ericaceae*, *Fabaceae*, *Plantaginaceae*, *Zygophyllaceae*, etc. (compare HORAK & KINZEL 1971, KINZEL 1982, ALBERT 1982, KÖNIGSHOFER & KINZEL 1986, POLLACK & ALBERT 1990, KINZEL & LECHNER 1992, KINZEL & BERGER 1992, KÄSTENBAUER 1992, HÜTTERER & ALBERT 1993, HERTENBERGER 1993, PFUNDNER 1993). The family of *Chenopodiaceae* is an impressive example: a high storage capacity for inorganic ions (especially alkali cations, chloride, nitrate and sulphate), oxalate synthesis, and a ubiquitous occurrence of glycinebetaine enable many representatives of this family to grow on dry and saline habitats (ALBERT & POPP 1977, OSMOND & al. 1980,

STEINER & KINZEL 1980, ALBERT 1982, KINZEL 1982, FLOWERS & YEO 1988, REIMANN 1992, HÜTTERER & ALBERT 1993). With a few exceptions (e.g. *Gypsophila*, which is a calcitrophic genus; HORAK 1971), *Caryophyllaceae* are oxalate-types (being "physiologically calciophobic" in the sense of ILJIN; cf. KINZEL 1963, 1982), thus representing a uniform physiotype which, in contrast to *Chenopodiaceae*, shows less preference for storage of inorganic ions and contain pinitol as a stress metabolite.

According to KÖNIGSHOFER & KINZEL 1986, at least two physiological features of the *Plantago* species may be of ecological significance. On the one hand, the ability to accumulate soluble Ca^{2+} in high concentrations as an osmotically active ion within the vacuoles might support the plants to cope with dry limestone habitats. On the other hand, the general physiological disposition to store large amounts of Cl^- and SO_4^{2-} probably promotes the adaptation to ruderal and saline environments. Members of another family, *Boraginaceae*, regularly contain three classes of substance: water-soluble pectin, the cyclitol D-bornesitol, and fructans (POLLACK & ALBERT 1990). These compounds probably act together to delicately regulate both storage and osmotic capacities, enabling members of this family to inhabit very dry habitats including deserts.

Fabaceae also show common physiological peculiarities. Characteristic features of this physiotype (which probably can be extended to all *Leguminosae*) are a tendency to accumulate divalent ions in the cell saps (calcitrophic plant types), a relatively high content of soluble carbohydrates and sugar alcohols (where pinitol may serve as a cytoplasmic and vacuolar osmoticum), and high levels of organic acids, of which malonic acid is a typical component. Additionally, on saline soils, *Leguminosae* exclude Na^+ from being taken up in greater amounts or retain Na^+ in the lower plant parts (ALBERT 1982, HÜTTERER & ALBERT 1993). Therefore, it is assumed that the physiological basis to overcome drought and salinity stress at least partially lies in effective salt (esp. Na^+) regulation and pinitol accumulation, respectively.

Pinitol and some other cyclitols assumed to function as compatible solutes (see above) are characteristic compounds also within the genus *Artemisia*, species of which are dominant constituents of shrub communities in semiarid and arid areas (ENGLMAIER & al. 1984). Moreover, xerophytic representatives of quite a number of plant families, having evolved successfully into desert biomes, accumulate sugar alcohols – mostly cyclitols (e.g. *Caryophyllaceae*, *Thymelaeaceae*, *Euphorbiaceae*, *Apiaceae*, *Boraginaceae*, *Bignoniaceae*, *Apocynaceae*, *Plantaginaceae*). Other drought tolerant taxa use the amino acid proline (*Brassicaceae*, *Tamaricaceae*) or betaines (*Amaranthaceae*, *Chenopodiaceae*, *Capparidaceae*, *Lamiaceae*) as presumable compatible solutes. Moreover, there are outstanding similarities of the pattern of these compounds between

xerophytes and halophytes, reflecting taxonomical characteristics (KÄSTENBAUER 1992, HERTENBERGER 1993, PFUNDNER 1993, POPP & ALBERT 1995). The fact that members of some particularly drought and/or salt tolerant families synthesize solutes of two (cyclitols and proline: *Aizoaceae*, *Leguminosae*, *Zygophyllaceae*) or three (cyclitols, proline and betaines: *Plumbaginaceae*, *Compositae*) different chemical classes highlights their outstanding ecophysiological significance (see also SMIRNOFF 1995).

Other examples of physiological traits with obvious ecological implications are the pronounced calcitrophy of *Brassicaceae* and *Crassulaceae* (more soluble Ca^{2+} than K^+ within cells, even on soils poor in Ca; refer to HORAK 1971, KINZEL 1982, RÖSSNER & POPP 1986, KINZEL & BERGER 1992) and Mn-accumulation (probably as soluble chelates) and an exclusively NH_4^+ utilizing system in *Ericaceae* (EDER 1980, KINZEL 1982, RUNGE 1983, KORCAK 1988).

On the other hand, beech (*Fagus sylvatica*) and Norway spruce (*Picea abies*) show a high flexibility in the mineral ion contents and ionic balance within their leaves, depending on specific habitat conditions (ALBERT & HÜBLER 1987, ALBERT 1989, ALBERT & PESCOLLER-TIEFENTHALER 1992). This is obviously quite an opposite strategy to face different habitat conditions as compared to the rather uniform "physiotypical" responses of certain taxa as mentioned above. More research is needed for a better understanding of this high nutritional plasticity.

In contrast to the dicotyledonous plant families, certain monocotyledonous families (*Cyperaceae*, *Juncaceae*, *Poaceae*) with often xeromorphic leaf structures show a very distinct type of mineral metabolism. They are generally poor in ions and exhibit a relative dominance of K^+ . Compared with dicots, plants belonging to these families efficiently exclude ballast ions (Ca^{2+} , Na^+ , heavy metals, etc.) and as a whole, appear to regulate their mineral metabolism more effectively (ALBERT 1982, KINZEL 1982). The genus *Carex* and some other representatives of *Cyperaceae*, for example, could especially well regulate their mineral metabolism, being excluders in ion-rich and accumulators in ion-poor habitats. Even under conditions of extremely low mineral nutrient availability (e.g. oligotrophic bogs), these plants still take up sufficient ions, due to highly active ion uptake systems, and utilize nutrient elements quite efficiently (ATWELL & al. 1980, VEERKAMP & al. 1980, VEERKAMP & KUIPER 1982a, b, VAN DER WERF & al. 1988, JONASSON & CHAPIN 1991, KROEHLER & LINKINS 1991, CHOO 1995). On the other hand, the halophytic species *Carex distans* maintains a very low Na^+ content even in salt-rich habitats (ALBERT & POPP 1977, HÜTTERER & ALBERT 1993, CHOO 1995). It is therefore regarded as a typical "salt excluder", as observed in some other members of that family (e.g. *Cyperus involucratus*; HOCKING 1985). This special pattern of physiological attributes undoubtedly is a solid basis for an understanding of the ecological success of

the genus *Carex* in a broad variety of habitat types (CHOO 1995). According to STEWART & al. 1979, ALBERT & POPP 1978, POPP & ALBERT 1980, and CHOO 1995, halophilic *Cyperaceae* and *Juncaceae* show only low concentrations of compatible solutes, which obviously is in accordance with their low salt levels. However, members of these families accumulate more soluble carbohydrates (especially fructose, glucose and sucrose) than dicotyledonous families in order to maintain a sufficiently low osmotic potential on saline habitats (ALBERT & POPP 1978, HÜTTERER & ALBERT 1993, CHOO 1995). Concerning organic acids, mainly citrate, malate and malonate are involved in balancing excess cation uptake in *Carex* species (CHOO 1995), and despite growing under very different ecological conditions, these plants also show rather constant organic acid levels (WOLLENWEBER 1987). Unlike in *Carex*, t-aconitate is typical in *Poaceae* (NIERHAUS & KINZEL 1971).

Considering the striking physiological similarities mentioned above, ALBERT & KINZEL 1973 proposed the rather xeromorphic monocots to be a uniform "physiotype" in terms of general ion poverty, K^+ -preponderance and high content of soluble carbohydrates acting as organic osmotica. However, with respect to nitrogen (refer to SALSAC & al. 1987, KLEINHOF & WARNER 1990, CHOO 1995), *Cyperaceae* use both forms of inorganic nitrogen; thus, they show a certain plasticity which is independent of leaf age, external conditions (especially acidity and anaerobic state of the root medium), and actual supply of nitrate (JANIESCH 1981, 1986, 1991, VAN DER WERF & al. 1988, MOOG & JANIESCH 1989, KONINGS & al. 1989, JONSDOTTIR & CALLAGHAN 1990, KOCH & al. 1991). In this point, *Cyperaceae* are apparently similar to *Poaceae* (GIGON & RORISON 1972, RORISON 1987, SALSAC & al. 1987, DE ARMAS & al. 1992, JACKSON & VOLK 1992), but contrast sharply with *Ericaceae* growing on similar habitat complexes (especially acidic-oligotrophic mires), which have largely lost the ability of nitrate assimilation, and have developed a preferential uptake of the reduced form of inorganic nitrogen (see above). In addition, as already mentioned, *Ericaceae* also show Mn accumulation. Both features agree with the preference of this family to grow in acidic and nutrient-poor habitat.

Conclusion

Towards an understanding of the ecological behaviour of a taxon (species, genus, family, etc.), the overall physiology of the taxon must be taken into account. Although the physiotype concept originally focused on mineral and organic acid metabolism, its reasonable application requires the consideration of as many physiological attributes as possible. Among physiological traits which enable certain plants to cope successfully with their environment, characteristics of the nitrogen metabolism, and the ability to accumulate low molecular weight organic solutes, as well as to synthesize bioactive natural compounds must be taken into account. Fur-

thermore, to characterize a certain plant taxon in a holistic approach, the combination of physiological and biochemical with morphological and anatomical features has to be considered.

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