Revista Brasil. Bot., V.27, n.1, p.1-10, jan.-mar. 2004

Review paper/Artigo de revisão

Ecophysiology

ULRICH LÜTTGE[1,3] and FABIO R. SCARANO[2]

(received: July 26, 2003; accepted: November 27, 2003)

ABSTRACT – (Ecophysiology). An attempt to delineate rather than to precisely define what we mean by ”ecophysiology“ is based on a brief historical overview of what eventually led to development of instrumentation and sampling strategies for analyses that allow description of physiological performance in the field. These techniques are surveyed. Ecophysiology originally is aut-ecology dedicated to the behaviour of individual plants, species or higher taxa, viz. “physiotypes”, in particular habitats. Examples of ecophysiological diversity are developed, which illustrate gradual merging with more integrative considerations of functions and dynamics of habitats or ecosystems, *i.e.* a trend of research towards physiological syn-ecology. The latter is exemplified by studies with comparisons of a variety of morphotypes and physiotypes within a given habitat or ecosystem and across a range of habitats or ecosystems. The high demand and complexity as well as the excitement of ecology and ecophysiology arise from the quest to cover **all** conditions of the existence of organisms according to Ernst Haeckel´s original definition of “ecology”.

Key words - ecological history, ecological integration, ecophysiology, physiological syn-ecology

RESUMO – (Ecofisiologia). Esta revisão procura delinear ao invés de precisamente definir o significado do termo “ecofisiologia”, com base em um breve apanhado histórico do desenvolvimento da instrumentação e de estratégias de amostragem para análises que permitam a descrição de desempenho fisiológico em condições de campo. Ecofisiologia originariamente é auto-ecologia dedicada ao comportamento de plantas individuais, espécies ou táxons superiores, viz. “fisiotipos”, em determinados habitats. Exemplos de diversidade ecofisiológica são tratados e ilustram a gradual integração desta disciplina com aspectos referentes ao funcionamento e dinâmica de habitats ou ecossistemas, *i.e.*, uma tendência de pesquisas voltadas para uma “sinecologia fisiológica”. Estudos que comparam uma gama de morfotipos e fisiotipos dentro de um dado habitat ou ecossistema ou entre habitats ou ecossistemas são exemplos deste caso. A complexidade e o encantamento da ecologia e da ecofisiologia emergem justamente da necessidade de cobrir **todas** as condições de existência dos organismos, de acordo com a definição original de “ecologia” de Ernst Haeckel.

Palavras-chaves - ecofisiologia, história da ecologia, integração ecológica, sinecologia fisiológica

Introduction: historical reminiscence and definitions

ECOLOGY is:

> *“The entire science of the relations of the organism to its surrounding environment, comprising in a broader sense all conditions of its existence.”*
>
> ERNST HAECKEL
>
> (“Die gesamte Wissenschaft von den Beziehungen des Organismus zur umgebenden Außenwelt, wohin wir im weiteren Sinne alle Existenzbedingungen rechnen können.”)

> *“…… a label for anything good that happens far from cities or anything that does not have synthetic chemicals in it.”*
>
> STEPHEN JAY GOULD

What is “ecophysiology”? Are we sure what we mean by “ecology”? The original definition is by Ernst Haeckel (1834-1919), who coined the term in 1866, about which Stephen Jay Gould (1977) writes as follows:

> *“Ernst Haeckel, the great popularizer of evolutionary theory in Germany, loved to coin words. The vast majority of his creations died with him half a century ago, but among the survivors are ‘ontogeny’, ‘phylogeny’, and ‘ecology’. The last is now facing an opposite fate - loss of meaning by extension and vastly inflated currency.”*

However, Haeckel’s original definition itself, as we see, was already quite broad and may help us to trace

---

1. Darmstadt University of Technology, Institute of Botany, Schittspahnstr. 3-5, D-64289, Darmstadt, Germany
2. Universidade Federal do Rio de Janeiro, CCS, IB, Dept Ecologia, Caixa Postal 68020, 21941-970 Rio de Janeiro, RJ
3. Corresponding author: luettge@bio.tu-darmstadt.de

the development of approaches in history. Alexander von Humboldt (1769 -1859) became the founder of plant geography, as he discovered that the physiognomy of vegetation is determined by environmental conditions and that the distribution of plants depends on the climate (von Humboldt 1808, ed. 1982). The impact of environmental factors on organisms then also became an essential aspect of natural selection in Charles Darwin's theory of evolution (Darwin 1859). Subsequently, having Haeckel's term "ecology", Andreas Franz Wilhelm Schimper (1856-1901), who was widely travelled in the tropics, founded "plant geography on an ecological basis" (Schimper 1898); and he also recognized the need for physiological experimentation:

> *"…the oecology of plant-distribution will succeed in opening new paths on condition only that it leans closely on experimental physiology, for it presupposes accurate knowledge of the conditions of the life of plants which experiment alone can bestow"*

(see introduction in Lange *et al*. 1981). Thus, Pickett *et al*. (1994) propose that ecology emerged out of the need highlighted by Schimper to integrate physiology and biogeography. Simon Schwendener (1829-1919) suggested that the relations between the environment and the morphological habit of plants are best studied in regions subject to extreme conditions. Finally, as the founder of ecophysiology we may consider Ernst Stahl (1848-1919) who introduced experimentation to ecological research. (For details see Mägdefrau 1992; for review see introduction in Lange *et al*. 1981, and Lüttge 1997a).

Some of this reasoning considers wider areas and geographical dimensions while some is dedicated to individual organisms and plants. Currently we distinguish "syn-ecology" and "aut-ecology", where the former applies to the ecology of habitats and entire ecosystems with a comprehensive view of all life ("syn-") and the latter to the ecology of organisms by themselves ("aut-")

In the first part of the 20th century researchers, such as Otto Stocker (1888-1979) and Bruno Huber (1899-1969), much promoted ecophysiology of plants because they developed instruments that could be taken to the field to measure the actual behaviour of plants under natural environmental conditions, especially to follow photosynthesis and transpiration. Simultaneously, the approach of studying adaptive functional traits of plants in the field also developed a strong tradition in Brazil. Paulo de Tarso Alvim, Karl Arens, Leopoldo Magno Coutinho, Mário Guimarães Ferri, Luiz Gouvêa Labouriau, to name but a few, were some of the Brazilian ecophysiologists active from the 1960ies onwards who left an important legacy (Alvim & Alvim 1976, Arens 1958 a, b, Coutinho 1990, Ferri 1944, Goodland & Ferri 1979, Labouriau 1966).

Increasing sophistication and demand of understanding has made it necessary to apply a kind of "ping-pong" between studies in the field and in laboratories, growth chambers and phytotrons with controlled environment. Problems of environmental adaptation, often in Simon Schwendener´s sense under particularly extreme conditions, are determined in the field. Physiological, biochemical and now also molecular mechanisms putatively favourable for adaptation to these conditions are assessed in the laboratory. Their actual action and effectiveness then must again be tested in the field, since it is not always given that traits intuitively considered favourable for ecological adaptation correlate with actual ecological distribution of plants. This casts questions back to laboratory work on individual plants, and so forth. Such approaches have been extremely successful making very important contributions to pinpointing physiological, biochemical and molecular bases of ecological adaptation. This created a voluminous international literature (*e.g.*, Lange *et al*. 1981, 1982, 1983a, b, Crawford 1989, Schulze & Caldwell 1994, Lüttge 1997a, Lambers *et al*. 1998, Larcher 2003, and many volumes of the series "Ecological Studies", Springer-Verlag, Berlin). In Brazil, Scarano & Franco (1998) organised a book that reviews adaptation of Brazilian plants to drought and flooding, which included contributions of some of the main active ecophysiologists from Brazil and also Venezuela. Of course, most of this is work on individual plants, hence aut-ecology. And indeed, among outdoor naturalists and ecologists with the quest of understanding habitat dynamics and ecosystems this has the odour of inadequate reductionism. Only recently, with the miniaturization and increasing facilitation of handling field-fit equipment it is getting possible to bridge the gap between syn- and aut-ecology, when many different species and life forms can be measured physiologically on site in a given habitat and comparisons can be made across different sites and habitats.

Field-fit equipment for plant ecophysiology

Basically any equipment that is portable or mobile enough and can be operated in the field can be used for on-site ecophysiological measurements, while - naturally -

restrictions for the glasshouse and growth-chamber part in the above-mentioned "ping-pong" are much less severe. However, this is stated much more readily than in fact put to action. It was already evident in Stocker's and Huber's early days of increasingly sophisticated field ecophysiology that special technical developments were important for field application. The major objectives then, as still mostly today, were to understand water relations and CO_2-assimilation, *i.e.* transpiration and CO_2-uptake. It was also realized that it was important to make momentary measurements of CO_2 and H_2O-vapour gas-exchange which avoided artefacts due to enclosure of plant parts, mostly leaves, in cuvettes. Stocker and associates used highly sensitive torsion-balances to very quickly measure transpiratory water loss from momentarily excised leaves. Stocker and Huber developed a photosynthesis-apparatus for field measurements of CO_2-exchange based on CO_2 absorption by NaOH with measurements of the electrical conductivity of the NaOH-solution. For a long time this was superior to IRGA (infra red gas analysis), which was restricted to climate controlled chambers and needed leaf-enclosure in gas-exchange cuvettes (Holdheide *et al.* 1936, Stocker & Vieweg 1960). Stocker packed all equipment available into a vehicle that was the first measuring-van and was used to study ecophysiology of desert plants in Mauritania (see Lüttge 1979). The principle of a mobile measuring-van was subsequently developed much further, especially by Otto L. Lange. In Brazil, Luiz G. Labouriau transformed a bus into a mobile laboratory in the early nineteen-sixties.

However, this raises another question: Which sites are accessible for ecophysiological measurements in the field? Measuring-vans at least need some kind of access roads. Special ecosystems will require particular approaches of access. As an example one important development currently are attempts for reaching forest canopies, much including tropical rainforests, for ecophysiological studies (Sutton 2001). Approaches of access range from rope-climbing techniques, fixed ladders, masts and platforms (Reitmayer *et al.* 2002), canopy walkways, cranes, balloon operated platforms up to a new high-tech canopy observation permanent access system (COPAS) with a gondola operating in all three dimensions of space (Gottsberger & Döring 1995, Ulmer Universitätsmagazin 2000).

Another very important trend is miniaturizing of equipment. The concept of the click-cuvette with an automatically or hand-operated opening and closing of a lid as developed by Lange (1962) to reduce and even avoid cuvette artefacts, *i.e.* the so-called cuvette-climate, together with the progress of micro-electronics is now providing us with increasingly smaller and readily portable instruments to perform IRGA-based measurements of gas exchange, *i.e.* H_2O-vapour and CO_2-fluxes, with porometers now available from various suppliers.

Miniaturization has also affected instruments measuring photosynthetic quantum yield, *i.e.* efficiency of light-use in photosynthesis, based on the Kautsky effect. We must remember that in the 1930ies H. Kautsky had to work at 73 K and in a dark room with elaborate optical setups. Now we use pulse amplitude modulated (PAM) fluorometers, which allow us to measure the far-red shifted chlorophyll fluorescence at ambient temperature and solar irradiation. Such fluorometers have been miniaturized to readily portable instruments (Mini-PAM; H. Walz, Effeltrich, Germany) providing information on potential and effective quantum yield and allowing calculations of apparent electron transport rates and non-photochemical effects of photosynthesis (Genty *et al.* 1989, van Kooten & Snel 1990, Schreiber & Bilger 1993, Bilger *et al.* 1995). Field equipment for measuring water potentials are Scholander-Hamel pressure chambers (Slavik 1974, Steudle 1987, 2001) and psycrometry based instruments, the latter also being applicable to measuring soil water potentials (Slavik 1974). Instruments for measuring xylem sap flow in stems of plants in the field based on heat pulse propagation originally introduced by Bruno Huber (Huber 1932, 1956, Vieweg & Ziegler 1960) are now also on the market.

Together, these approaches now permit to obtain extensive and comprehensive sets of data on water relations and photosynthesis under actual environmental conditions in the field. The easiness of equipment-use now even bears a danger of non-critical accumulation of vast amounts of data. This certainly constitutes a strong demand on problem-oriented intuition by ecophysiological researchers in the field. It also increasingly requires adoption of theoretical approaches of data analysis (Hütt & Lüttge 2002).

Furthermore sampling strategies for various analyses in the laboratory are now more than a supplement to instrument-based field ecophysiology. This comprises sampling various compartments, such as roots, stems, leaves, xylem, phloem etc., and also soil, and analyses of contents of mineral nutrients and metabolites and stable isotopes (mainly ^{2}H, ^{13}C, ^{15}N, ^{18}O) (*e.g.*, Scarano *et al. in press*). While for some purposes air dried material is sufficient (mineral contents, stable isotopes), special field sampling is also required (metabolites) with rapid microwave oven drying and/or storage on dry ice or best in liquid nitrogen. A very powerful new approach supplementing ecophysiology is taking samples for isolating molecular markers (DNA) allowing to link population genetics to comparison of ecophysiological traits (*e.g.*, Vaasen *et al.* 2002, Gehrig *et al.* 2003).

Such analyses of field-sampled specimen in the laboratory must not be confused with the field-laboratory "ping-pong" discussed above. They are directly interwoven with the field measurements. The ensemble of such analyses, however, regularly very strongly enhances conclusiveness of field measurements. This now is threatened, however, in a rather uncaring way. Sample analysis often requires a somewhat sophisticated high-tech laboratory background, which frequently needs specialization with respect to investments and equipment. This is not always available at the places of sample-generation and thus makes transport of samples necessary, which may include crossing national borders. While on one hand all ecologists, including ecophysiologists, must and do welcome legislation protecting national privileges in control and maintenance of biodiversity, on the other hand restrictive handling and a lack of clear regulations for scientific cooperation in many cases begin to hamper progress of ecophysiological research severely.

Examples of aut-ecological studies

Examples of aut-ecological studies can be listed by i) special adaptations and ii) special habitats with particular stresses and combinations of stresses.

(i) Considering adaptations, the term "physiotype" propagated by Kinzel (1972, 1982) appears to be very useful. The physiotype *sensu* Kinzel is the complement of all properties or traits that is shared by individuals belonging to a taxonomical unit, where these taxa may represent different levels, *i.e.* species, genera, families, orders or even higher taxa. The respective properties are, *e.g.*, given preferences, resistances and sensitivities, and their combinations. Kinzel and collaborators have exemplified physiotypes mostly on the basis of mineral relations, typical physiotypes being, *e.g.*, calcicole and calcifuge plants, halophytes, heavy metal accumulators, nitrophilous plants and their subtypes. However, since this can be extended to any kind of stress factor ("stressor") examples of special physiological adaptations are manifold, almost infinite. Plants studied aut-ecologically range over all major groups, from cyanobacteria (Lüttge *et al.* 1995, Lüttge 1997b, Rascher *et al.* 2003) and lichens (Lange 1992) to higher plants. Studies are often specially dedicated to light use, *i.e.* to photosynthesis and photoinhibition, and great themes of ecophysiology are, *e.g.*, the midday-depression of C_3-photosynthesis (Schulze & Hall 1982), C_4-photosynthesis (Ray & Black 1979, Osmond *et al.* 1980), crassulacean acid metabolism (CAM) and C_3-CAM-switches (Winter & Smith 1996, Functional Plant Biology 2002) all related to stress given by availability of water (Lange *et al.* 1976), and hence, the major topics and concerns of plant ecophysiology (see above: historical reminiscence).

(ii) The use of habitats for performing aut-ecological studies often reflects Simon Schwendener's advice that studies may be best performed in regions providing extreme conditions (see above: historical reminiscence). Thus, typical ecophysiological study sites comprise deserts and other arid environments, salinas, and other salinity affected environments, various tropical habitats, such as rain-forests, savannas (Franco 2002), mangroves (Trees 2002) and inselbergs (Porembski & Barthlott 2000), flooded habitats (Joly 1994), high latitudes (arctic and antarctic; Crawford 1989) and altitudes (alpine zones of mountains, paramos; Rundel *et al.* 1994), more recently also forest canopies (Linsenmair *et al.* 2001), and many others.

Ecophysiological diversity

To address the question of ecophysiological diversity again the physiotype-concept appears useful. Just like comparative morphology and anatomy delineate different structural life forms or morphotypes, comparative physiology, biochemistry, biophysics and molecular biology delineate different physiological life forms or physiotypes. Briefly, the complete set of phenotypical traits generated by a genotype in the morphological domain is the morphotype and in the physiological domain is the physiotype. Although physiotypical traits basically often provide a good explanation of the occurrence of plants in habitats, it is impossible to derive strict rules. For example, morphologically almost identical rosettes of epiphytic bromeliad species can be found side by side on the same branch of a phorophyte, one being an obligate C_3- the other one an obligate CAM-species (Griffiths *et al.* 1986). Morphologically very similar rosettes of the two C_3-species *Paepalanthus polyanthus* Kunth (Eriocaulaceae) and *Eryngium eurycephalum* Malme (Apiaceae) growing next to each other were observed to differ in susceptibility to photoinhibition and nitrogen-nutrition signature (Scarano *et al.* 2001).

Physiological and ecological optima are not necessarily congruent (page 222 in Kinzel 1982). Ecophysiological plasticity determines the width of functional niches. Thus, for example, it was shown that the niche-width of the obligate C_3-species *Clusia multiflora* H.B.K. (Clusiaceae) is smaller than that of the C_3/CAM-intermediate species *Clusia minor* L. (Clusiaceae). Counterintuitively, *i.e.* when CAM is considered an adaptation to critical water supply, C_3-*C. multiflora* may dominate open exposed sites and does not occur in shaded sites, while its compatriot the C_3-CAM-intermediate *C. minor* occupies shaded sites and also intrudes the exposed sites of *C. multiflora*. Not the water saving mechanism of CAM *per se* but the flexibility given by CAM appears to be the specific advantage of *C. minor* (Herzog *et al.* 1999, Lüttge 2000). As another example, small-scale patchy habitat segregation was also explained physiologically for a C_3 and a CAM species of the bromeliad genus *Nidularium* (Bromeliaceae) in the understory of a tropical swamp forest (Scarano *et al.* 1999). The C_3-species *N. innocentii* Lem. is restricted to shaded periodically flooded patches and the CAM-species *N. procerum* Lindm. to semi-exposed permanently flooded patches, with CAM allowing colonization of patches potentially exposed to higher irradiance. Habitat preferences of tree and palm species between neighbouring longer-term and shorter-term flooding sites, in an estuarine várzea forest in the Amazon, were often related to patterns of carbohydrate storage in roots of saplings prior to flooding (Scarano *et al.* 1994). For a further example, two giant rosette plants, the two C_3-species *Lobelia gibberoa* Hemsl. (Lobeliaceae) and *Solanecio gigas* (Vatke) C. Jeffrey (Asteraceae) in an afromontane forest valley, it was found that niche occupation could be explained by a combination of morphological and anatomical traits and ecophysiological features. Transpiration and photosynthesis were basically similar in both species but responses to varying soil moisture differed. *L. gibberoa* had a well-developed vascular cylinder but maintained a large number of rosettes on one plant and a large average leaf area index (LAI). It was restricted to the more humid parts of the valley. *S. gigas*, having a poorly developed vascular bundle had many fewer rosettes and a lower average LAI and was more flexible occupying both the wetter and the drier locations in the valley (Lüttge *et al.* 2001).

These examples, taken from our work, although still largely physiological aut-ecology already lead to physiological syn-ecology as they combine aut-ecology with describing functions and dynamics in habitats and ecosystems.

It was also debated whether plasticity may support development of species diversity. Plasticity may either hinder speciation by protecting given genotypes from selection under environmental pressure, or enhance speciation by allowing large ecological amplitudes (but see Schlichting & Pigliucci 1998). Ecological amplitudes may separate populations with reduced sets of genotypes specially adapted to particular sites leading to genetically stable populations, which we call ecotypes (Turesson 1922, Kinzel 1982). Segregation may then enhance speciation, as exemplified by discussing the large ecological amplitude and species richness of the genus *Clusia* (Lüttge 1999, 2000). In this context it is very important that molecular studies of population genetics now can be combined with ecophysiological measurements, because variations of physiotype may even occur between populations, and it is most regrettable when bureaucratic constraints hinder this approach (see above: field-fit equipment and sampling).

Physiological syn-ecology

As argued in the Introduction physiological syn-ecology is a newly emerging field, and this is particularly due to the great progress in development of miniaturized field-fit equipment. Physiological syn-ecology is comparative ecophysiology. Hence, in this case, one would not wish to exaggerate obedience to Simon Schwendener's suggestion because extreme sites will be occupied by only very few specialists adapted to the dominating stressor, and the attempts of physiological syn-ecology rapidly return to aut-ecology. Not too extreme sites with a diversity of species with different adaptive strategies appear more suitable. It depends on specific examples though. On the very extreme habitat of the highly sun-exposed bare granite surface of tropical rock outcrops (inselbergs) the distribution of cyanobacteria communities building up the rock-surface ecosystem can largely be explained by physiological traits of light and water use (Büdel *et al.* 1994, Rascher *et al.* 2003). Such "ink-stripe"-like cyanobacterial ecosystems (Lüttge 1997b) appear to be rather simple, but the various types of related soil crusts - perhaps overall in somewhat less extreme situations - are highly diverse in species of cyanobacteria, algae, fungi, bryophytes, and small animals and largely characterized ecophysiologically (Belnap & Lange 2001).

For higher plants we began to undertake attempts to combine habitat and species comparisons in comparative ecophysiology for advancing physiological syn-ecology. This is a long-term programme starting with i) the comparison of various elements of xerophytic and halophytic vegetation of a coastal alluvial plain in Northern Venezuela looking at small ground-covering halophytes, mangroves, epiphytic and terrestrial bromeliads, orchids, and cacti (Griffiths *et al.* 1989, Lee *et al.* 1989, Lüttge *et al.* 1989a, b, Medina *et al.* 1989, Smith *et al.* 1989), and moving on to ii) a comparison of various morphotypes and physiotypes, viz. woody plants, climbers, graminoids, rosettes, cacti and geophytes, along a gradient of sites marginal to the Atlantic rain forest in Brazil, viz. dry and wet restingas, dry forest, and high altitude fields (Scarano *et al. in press*), and iii) an increasingly comprehensive range of measurements and analyses including photosynthesis, stable isotopes, metabolites and various plant organs such as leaves, roots, wood, xylem, phloem, etc.

A particularly interesting example of physiological syn-ecology is the study of differential effects of dry-season drought on seedling performance in co-occurring tropical moist forest plants in a semi-deciduous forest in Panamá (B. Engelbrecht, data not published, Engelbrecht & Kursar 2003). The study uses experimental plots with transplantation strategies as well as the natural rainfall gradient across the Panamanian isthmus from the wetter Atlantic to the drier Pacific side. Many traits that are often intuitively considered to be bases of drought adaptation and resistance did not individually correlate with plant distribution. Species' differences in drought resistance were associated with a wide range of combinations of morphological and physiological characters. Maintenance of critical leaf-water potential appeared to be the most essential factor.

Epilogue: a need for integration

Schimper's (1898) urge to integrate plant geography and physiology as a means to understand plant distribution and abundance patterns is still largely unfulfilled. Although some new workable hypotheses emerge (*e.g.*, Scarano 2002), results on a given scale do not always become confirmed generalisations as we enhance the scale. For instance, our latest study on plants of several marginal habitats of the Atlantic rainforest complex in the state of Rio de Janeiro (Scarano *et al. in press*) showed a few trends, but no confirmable generalisation: (1) at the intra-specific level, ecophysiological performance often (but not always) varied largely in both time and space; (2) at the inter-specific level, ecophysiological performance was often (but not always) related to species dominance in the community; (3) at both intra- and inter-specific level, ecophysiological performance was not related to the geographic distribution patterns, *i.e.*, generalists and specialists did not form groups of similarly behaving plants in regard to ecophysiology. Confirmed generalisations shall be necessary to help us formulate models and theories to explain ecological and ecophysiological diversity on a geographical scale (see Pickett *et al.* 1994), which will provide the necessary background to understanding processes such as speciation and extinction, essential for correct conservation and management initiatives. Thus, it appears that in order to search for general patterns, physiological syn-ecology studies should try to enhance the x, y and z axis of their orientations, *i.e.*, increase the number of species sampled, increase the spatial and temporal scales covered and increase the numbers and kinds of parameters at different ecological hierarchical scales for each species.

While confirmed generalisations do not fully emerge from our integration initiatives on a geographical scale, some case studies in a narrower geographical range indicate the potential of integrated studies. For instance, Scarano *et al.* (2002) compared four neighbouring populations of *Aechmea bromeliifolia* (Rudge) Baker (Bromeliaceae) under distinct selective pressures, and by combining parameters related to demography, growth, leaf anatomy and photochemical efficiency, they could tell which spectrum of the morpho-physiological variation found consisted in acclimation and which consisted in stress-symptom.

In conclusion, ecology in general and also ecophysiology are highly integrative sciences. They require integration of wide ranges of information input about the physical environment as well as parameters of biological diversity. They require work on a wide range of scaling levels extending over some 15 to 20 powers of 10 in space, *i.e.* from planet geographic levels and ecosystems to habitats and sites, plants, organs, cells, organelles, membranes and molecules, and in time, *i.e.* from slow developments of vegetation in time scales of centuries and decades down to rapid events, such as photosynthetic excitation in pico- and femto-seconds (Osmond *et al.* 1980, Lüttge 1996).

At the onset of Haeckel´s definition of ecology, *i.e.* "…. relations of the organism …..comprising ALL conditions of its existence", many argued that if Haeckel's definition was correct, "there is very little that is *not* ecology" (see Krebs 1972). It seems ironic that it took us more than a whole century to realise that Haeckel appears to be right after all: this makes ecology and ecophysiology both demanding and complexly difficult, therefore a very exciting challenge.

Acknowledgements – We thank S.M.C. Dietrich and M.S. Buckeridge for valuable comments on the manuscript and for providing relevant additional information about the history of ecophysiology in Brazil. This review was produced within the scope of the projects funded by The Volkswagen Foundation, Hannover, Germany and by the Brazilian Long Term Ecological Research Program (CNPq, Brazilian Research Council). F.R. Scarano thanks Capes (Brazilian Higher Education Council) for a post-doctoral grant in The University of Minnesota, USA, during the period he co-wrote this review.

References

ALVIM, P.T. & ALVIM, R. 1976. Relation of climate to growth periodicity in tropical trees. *In* Tropical trees as living systems (P.B. Tomlinson & M.H. Zimmermann, eds.). Cambridge University Press, Cambridge, p.455-464.

ARENS, K. 1958a. Considerações sôbre as causas do xeromorfismo foliar. Boletim da Faculdade de Filosofia Ciências e Letras da Universidade de São Paulo, Botânica 15:23-56.

ARENS, K. 1958b. O cerrado como vegetação oligotrófica. Boletim da Faculdade de Filosofia Ciências e Letras da Universidade de São Paulo, Botânica 15:59-77.

BELNAP, J. & LANGE, O.L. (eds.). 2001. Biological soil crusts: Structure, function, and management. Ecological Studies v. 150. Springer-Verlag, Berlin.

BILGER, W., SCHREIBER, U. & BOCK, M. 1995. Determination of the quantum efficiency of photosystem II and of non-photochemical quenching of chlorophyll fluorescence in the field. Oecologia 102:425-432.

BÜDEL, B., LÜTTGE, U., STELZER, R., HUBER, O. & MEDINA, E. 1994. Cyanobacteria of rocks and soils of the Orinoco lowlands and the Guayana uplands, Venezuela. Botanica Acta 107:422-431.

COUTINHO, L.M. 1990. Fire in the ecology of the Brazilian cerrado. *In* Fire in the tropical biota: ecosystem processes and global challenges (J.G. Goldammer, ed.). Springer-Verlag, Berlin, p.82-105.

CRAWFORD, R.M.M. 1989. Studies in plant survival. Blackwell, Oxford.

DARWIN, C. 1859. On the origin of species by means of natural selection. John Murray, London.

ENGELBRECHT, B.M. & KURSAR, T.A. 2003. Comparative drought resistance of seedlings of 28 species of co-occurring tropical woody plants. Oecologia 136:383-393.

FERRI, M.G. 1944. Transpiração de plantas permanentes dos "Cerrados". Boletim da Faculdade de Filosofia Ciências e Letras da Universidade de São Paulo, Botânica 4:161-224.

FRANCO, A.C. 2002. Ecophysiology of woody plants. *In* The cerrados of Brazil (P.S. Oliveira & R.J. Marquis, eds.). Columbia University Press, New York, p.178-197.

FUNCTIONAL PLANT BIOLOGY. 2002. Crassulacean acid metabolism. Special issue. Functional Plant Biology 29:657-785.

GEHRIG, H.H., ARANDA, J., CUSHMAN, M.A., VIRGO, A., CUSHMAN, J.C., HAMMEL, B.E. & WINTER, K. 2003. Cladogram of Panamanian *Clusia* based on nuclear DNA: Implications for the origins of Crassulacean Acid Metabolism. Plant Biology 5:59-70.

GENTY, B., BRIANTAIS, J.-M. & BAKER, N.R. 1989. The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. Biochimica Biophysica Acta 990:87-92.

GOODLAND, R. & FERRI, M.G. 1979. Ecologia do cerrado. Edusp, São Paulo.

GOTTSBERGER, G. & DÖRING, J. 1995. "COPAS", an innovative technology for long-term studies of tropical rain forest canopies. Phyton 35:165-173.

GOULD, S.J. 1977. Ever since Darwin. Reflections in natural history. Penguin Book, Harmondsworth.

GRIFFITHS, H., LÜTTGE, U., STIMMEL, K.-H., CROOK, C.E., GRIFFITHS, N.M. & SMITH, J.A.C. 1986. Comparative ecophysiology of CAM and C_3 bromeliads. III. Environmental influences on CO_2 assimilation and transpiration. Plant, Cell and Environment 9:385-393.

GRIFFITHS, H., SMITH, J.A.C., LÜTTGE, U., POPP, M., CRAM, W.J., DIAZ, M., LEE, H.S.J., MEDINA, E., SCHÄFER, C. & STIMMEL, K.-H. 1989. Ecophysiology of xerophytic and halophytic vegetation of a coastal alluvial plain in northern Venezuela. IV. *Tillandsia flexuosa* Sw. and *Schomburgkia humboldtiana* Reichb., epiphytic CAM plants. New Phytologist 111:273-282.

HAECKEL, E. 1866. Generelle Morphologie der Organismen: Allgemeine Grundzüge der organischen Formen-Wissenschaft, mechanisch begründet durch die von Charles Darwin reformirte Descendenz-Theorie. 2 vols. George Reimer, Berlin.

HERZOG, B., HOFFMANN, S., HARTUNG, W. & LÜTTGE, U.1999. Comparison of photosynthetic responses of the sympatric tropical C_3-species *Clusia multiflora* H.B.K. and the C_3-CAM intermediate species *Clusia minor* L. to irradiance and drought stress in a phytotron. Plant Biology 1:460-470.

HOLDHEIDE, W., HUBER, B. & STOCKER, O. 1936. Eine Feldmethode zur Bestimmung der momentanen Assimilationsgröße von Landpflanzen. Berichte der deutschen botanischen Gesellschaft 54:168-188.

HUBER, B. 1932. Beobachtung und Messung pflanzlicher Saftströme. Berichte der deutschen botanischen Gesellschaft 50:89-109.

HUBER, B. 1956. Die Gefäßleitung. *In* Handbuch der Pflanzenphysiologie (W. Ruhland, ed.). Springer-Verlag, Berlin, v.3, p.541-582.

HUMBOLDT, A. VON. 1982. Südamerikanische Reise. 1808. Quoted after the edition of Greno Verlagsgesellschaft mbH, Nördlingen.

HÜTT, M.-TH. & LÜTTGE, U. 2002. Nonlinear dynamics as a tool for data analysis and modeling in plant physiology. Plant Biology 4:281-297.

JOLY, C.A. 1994. Flooding tolerance: a reinterpretation of Crawford´s metabolic theory. Proceedings of the Royal Society of Edinburgh 102B:343-354.

KINZEL, H. 1972. Biochemische Pflanzenökologie. Schriften des Vereins zur Verbreitung naturwissenschaftlicher Kenntnisse in Wien 112:77-98.

KINZEL, H. 1982. Pflanzenökologie und Mineralstoffwechsel. Verlag Eugen Ulmer, Stuttgart.

KOOTEN, O. VAN & SNEL, J.F.H. 1990. The use of chlorophyll fluorescence nomenclature in plant stress physiology. Photosynthetic Research 25:147-150.

KREBS, C.J. 1972. Ecology: the experimental analysis of distribution and abundance. Harper & Row, New York.

LABOURIAU, L.G. 1966. Revisão da situação da ecologia vegetal nos cerrados. Anais da Academia Brasileira de Ciências 38:5-38.

LAMBERS, H., CHAPIN, F.S. & PONS, T.L. 1998. Plant physiological ecology. Springer-Verlag, Berlin.

LANGE, O.L. 1962. Eine “Klapp-Küvette” zur CO_2-Gaswechselregistrierung an Blättern von Freilandpflanzen mit dem URAS. Berichte der deutschen botanischen Gesellschaft 75:41-50.

LANGE, O.L. 1992. Pflanzenleben unter Stress. Flechten als Pioniere der Vegetation an Extremstandorten der Erde. Rostra Universitatis Wirceburgensis - VI, Würzburg.

LANGE, O.L., KAPPEN, L. & SCHULZE, E.-D. (eds.). 1976. Water and plant life. Ecological Studies, v.19. Springer-Verlag, Berlin.

LANGE, O.L., OSMOND, C.B., NOBEL, P. & ZIEGLER, H. (eds.). 1981. Physiological plant ecology I, Responses to the environment. Encyclopedia of Plant Physiology New Series, v.12 A. Springer-Verlag, Berlin.

LANGE, O.L., OSMOND, C.B., NOBEL, P. & ZIEGLER, H. (eds.). 1982. Physiological plant ecology II, Water relations and carbon assimilation. Encyclopedia of Plant Physiology New Series v.12 B. Springer-Verlag, Berlin.

LANGE, O.L., OSMOND, C.B., NOBEL, P. & ZIEGLER, H. (eds.). 1983a. Physiological plant ecology III, Responses to the chemical and biological environment. Encyclopedia of Plant Physiology New Series v.12 C. Springer-Verlag, Berlin.

LANGE, O.L., OSMOND, C.B., NOBEL, P. & ZIEGLER, H. (eds.). 1983b. Physiological plant ecology IV, Ecosystem processes: Mineral cycling, productivity and man´s influence. Encyclopedia of Plant Physiology New Series v.12 D. Springer-Verlag, Berlin.

LARCHER, W. 2003. Physiological plant ecology. Springer-Verlag, Berlin.

LEE, H.S.J., LÜTTGE, U., MEDINA, E., SMITH, J.A.C., CRAM, W.J., DIAZ, M., GRIFFITHS, H., POPP, M., STIMMEL, K.-H. & THONKE, B. 1989. Ecophysiology of xerophytic and halophytic vegetation of a coastal alluvial plain in northern Venezuela. III. *Bromelia humilis* Jacq., a terrestrial CAM bromeliad. New Phytologist 111:253-271.

LINSENMAIR, K.E., DAVIS, A.J., FIALA, B. & SPEIGHT, M.R. (eds.). 2001. Tropical forest canopies: Ecology and management. Kluwer Academic Publishers. Dordrecht.

LÜTTGE, U. 1979. Otto Stocker zum 90. Geburtstag. Berichte der deutschen botanischen Gesellschaft 92:1-6.

LÜTTGE, U. 1996. Up and down scalar levels: Reductionism or infinite fractal complexity in biology? European Review 4:329-332.

LÜTTGE, U. 1997a. Physiological ecology of tropical plants. Springer-Verlag, Berlin.

LÜTTGE, U. 1997b. Cyanobacterial Tintenstrich communities and their ecology. Naturwissenschaften 84:526-534.

LÜTTGE, U. 1999. One morphotype, three physiotypes: Sympatric species of *Clusia* with obligate C_3-photosynthesis, obligate CAM and C_3-CAM intermediate behaviour. Plant Biology 1:138-148.

LÜTTGE, U. 2000. Photosynthese-Physiotypen unter gleichen Morphotypen, Species und bei Klonen: Kann ökophysiologische Plastizität zur Entstehung von Diversität beitragen? Berichte der Reinhard Tüxen Gesellschaft 12:319-334.

LÜTTGE, U., BÜDEL, B., BALL, E., STRUBE, F. & WEBER, P. 1995. Photosynthesis of terrestrial cyanobacteria under light and desiccation stress as expressed by chlorophyll fluorescence and gas exchange. Journal of Experimental Botany 46:309-319.

LÜTTGE, U., FETENE, M., LIEBIG, M., RASCHER, U. & BECK, E. 2001. Ecophysiology of niche occupation by two giant rosette plants, *Lobelia gibberoa* Hemsl and *Solanecio gigas* (Vatke) C. Jeffrey, in an afromontane forest valley. Annals of Botany 88:267-278.

LÜTTGE, U., MEDINA, E., CRAM, W.J., LEE, H.S.J., POPP, M. & SMITH, J.A.C. 1989a. Ecophysiology of xerophytic and halophytic vegetation of a coastal alluvial plain in northern Venezuela. II. Cactaceae. New Phytologist 111:245-251.

LÜTTGE, U., POPP, M., MEDINA, E., CRAM, W.J., DIAZ, M., GRIFFITHS, H., LEE, H.S.J., SCHÄFER, C., SMITH, J.A.C. & STIMMEL, K.-H. 1989b. Ecophysiology of xerophytic and halophytic vegetation of a coastal alluvial plain in northern Venezuela. V. The *Batis maritima* - *Sesuvium portulacastrum* vegetation unit. New Phytologist 111:283-291.

MÄGDEFRAU, K. 1992. Geschichte der Botanik. Leben und Leistung großer Forscher. 2. G. Fischer, Stuttgart

MEDINA, E., CRAM, W.J., LEE, H.S.J., LÜTTGE, U., POPP, M., SMITH, J.A.C. & DIAZ, M. 1989. Ecophysiology of xerophytic and halophytic vegetation of a coastal alluvial plain in northern Venezuela. I. Site description and plant communities. New Phytologist 111:233-243.

OSMOND, C.B., BJÖRKMAN, O. & ANDERSON, D.J. 1980. Physiological processes in plant ecology. Ecological Studies v.36. Springer-Verlag, Berlin.

PICKETT, S.T.A., KOLASA, J. & JONES, C.G. 1994. Ecological understanding. Academic Press, New York.

POREMBSKI, S. & BARTHLOTT, W. 2000. Inselbergs. Ecological Studies v.146. Springer-Verlag, Berlin.

RASCHER, U., LAKATOS, M., BÜDEL, B. & LÜTTGE, U. 2003. Photosynthetic field capacity of cyanobacteria of a tropical inselberg of the Guyana highlands. European Journal of Phycology 38:247-256.

RAY, T.B. & BLACK, C.C. 1979. The C_4 pathway and its regulation. *In* Photosynthesis II, Photosynthetic carbon metabolism and related processes (M. Gibbs & E. Latzko, eds.). Encyclopedia of Plant Physiology new series Springer-Verlag, Berlin, v.6, p.77-101.

REITMAYER, H., WERNER, H. & FABIAN, P. 2002. A novel system for spectral analysis of solar radiation within a mixed beech-spruce stand. Plant Biology 4:228-233.

RUNDEL, P.W., SMITH, A.P. & MEINZER, F.C. (eds.). 1994. Tropical alpine environments. Plant form and function. Cambridge University Press, Cambridge.

SCARANO, F.R. 2002. Structure, function and floristic relationships of plant communities in stressful habitats marginal to the Brazilian Atlantic rainforest. Annals of Botany 90:517-524.

SCARANO, F.R. & FRANCO, A.C. (eds.). 1998. Ecophysiological strategies of xerophytic and amphibious plants in the neotropics. Series Oecologia Brasiliensis, v.4. PPGE-UFRJ, Rio de Janeiro.

SCARANO, F.R., CATTÂNIO, J.H. & CRAWFORD, R.M.M. 1994. Root carbohydrate storage in young saplings of an Amazonian tidal várzea forest before the onset of the wet season. Acta Botanica Brasilica 8:129-139.

SCARANO, F.R., MATTOS, E.A., FRANCO, A.C., HERZOG, B., BALL, E., GRAMS, T.E.E., MANTOVANI, A., BARRETO, S., HAAG-KERWER, A. & LÜTTGE, U. 1999. Habitat segregation of C_3 and CAM *Nidularium* (Bromeliaceae) in response to different light regimes in the understory of a swamp forest in southeastern Brazil. Flora 194:281-288.

SCARANO, F.R., DUARTE, H.M., RIBEIRO, K.T., RODRIGUES, P.J.F.P., BARCELLOS, E.M.B., FRANCO, A.C., BRULFERT, J., DELÉENS, E. & LÜTTGE, U. 2001. Four sites with contrasting environmental stress in southeastern Brazil: relations of species, life form diversity, and geographic distribution to ecophysiological parameters. Botanical Journal of the Linnean Society 136:345-364.

SCARANO, F.R., DUARTE, H.M., RÔÇAS, G., BARRETO, S.M.B., AMADO, E.F., REINERT, F., WENDT, T., MANTOVANI, A., LIMA, H.R.P. & BARROS, C.F. 2002. Acclimation or stress symptom? An integrated study of intraspecific variation in the clonal plant *Aechmea bromeliifolia*, a widespread CAM tank-bromeliad. Botanical Journal of the Linnean Society 140:391-401.

SCARANO, F.R., DUARTE, H.M., FRANCO, A.C., GESSLER, A., MATTOS, E.A., RENNENBERG, H. & LÜTTGE, U. Physiological synecology of tree species in relation to geographic distribution and ecophysiological parameters at the Atlantic forest periphery in Brazil: an overview. Trees, Structure and Function (in press)

SCHIMPER, A.F.W. 1898. Pflanzengeographie auf physiologischer Grundlage. Fischer, Jena.

SCHLICHTING, C.D. & PIGLIUCCI, M. 1998. Phenotypic evolution: a reaction norm perspective. Sinauer Associates, Sunderland.

SCHREIBER, U. & BILGER, W. 1993. Progress in chlorophyll fluorescence research: major developments during the past years in retrospect. Progress in Botany 54:151-172.

SCHULZE, E.-D. & CALDWELL, M.M. 1994. Ecophysiology of photosynthesis. Springer-Verlag, Berlin.

SCHULZE, E.-D. & HALL, A.E. 1982. Stomatal responses, water loss and CO_2 assimilation rates of plants in contrasting environments. *In* Physiological plant ecology II, Water relations and carbon assimilation. (O.L. Lange, C.B. Osmond, P. Nobel & H. Ziegler, eds.). Encyclopedia of Plant Physiology new series. Springer-Verlag, Berlin, v.12 B, p.181-230.

SLAVIK, B. 1974. Methods of studying plant water relations. Ecological Studies v.9. Springer-Verlag, Berlin.

SMITH, J.A.C., POPP, M., LÜTTGE, U., CRAM, W.J., DIAZ, M., GRIFFITHS, H., LEE, H.S.J., MEDINA, E., SCHÄFER, C., STIMMEL, K.-H. & THONKE, B. 1989. Ecophysiology of xerophytic and halophytic vegetation of a coastal alluvial plain in northern Venezuela. VI. Water relations and gas exchange of mangroves. New Phytologist 111:293-307.

STEUDLE, E. 1987. Pressure probe techniques: Some recent developments. *In* Proceedings of the International Conference on measurement of soil and plant water status (R.J. Hanks & R.W. Brown, eds.). Utah State University, Logan, p.183-191.

STEUDLE, E. 2001. The cohesion-tension mechanism and the acquisition of water by plant roots. Annual Review of Plant Physiology and Plant Molecular Biology 52:847-875.

STOCKER, O. & VIEWEG, G.-H. 1960. Die Darmstädter Apparatur zur Messung der Photosynthese unter ökologischen Bedingungen. Berichte der deutschen botanischen Gesellschaft 73:198-208.

SUTTON, S.L. 2001. Alice grows up: canopy science in transition from wonderland to reality. Plant Ecology 153:13-21.

TREES. 2002. Special issue mangroves. Trees, Structure and Function 16:63-243.

TURESSON, G. 1922. The genotypic response of the plant species to the habitat. Hereditas 3:211-350.

ULMER UNIVERSITÄTSMAGAZIN. 2000. Unerforschter "Kontinent": Mit COPAS in die Baumkronen des tropischen Regenwaldes. Uni Ulm Intern 30/237:18-20.

VAASEN, A., BEGEROW, D., LÜTTGE, U. & HAMPP, R. 2002. The genus *Clusia* L.: Molecular evidence for independent evolution of photosynthetic flexibility. Plant Biology 4:86-93.

VIEWEG, G.H. & ZIEGLER, H. 1960. Thermoelektrische Registrierung der Geschwindigkeit des Transpirationsstromes. Berichte der deutschen botanischen Gesellschaft 73:221-226.

WINTER, K. & SMITH, J.A.C. (eds.). 1996. Crassulacean acid metabolism. Biochemistry, ecophysiology and evolution. Ecological Studies v.11. Springer-Verlag, Berlin.