

Progress in Botany 80

Francisco M. Cánovas
Ulrich Lüttge
Rainer Matyssek
Hans Pretzsch *Editors*

Progress in Botany

 Springer

Progress in Botany

Volume 80

Series Editors

Ulrich Lüttge, TU Darmstadt,
FB Biologie (10), Schnittspahnstraße 3–5,
64287 Darmstadt, Germany

Francisco M. Cánovas
Universidad de Málaga, Depto. Biología
Molecular y Campus de Teatinos, 29071
Málaga, Spain

Rainer Matyssek
Technische Universität München
Hans-Carl-von-Carlowitz-Platz 2
Wissenschaftszentrum Weihenstephan
85354 Freising, Germany

Hans Pretzsch
Technische Universität München
Hans-Carl-von-Carlowitz-Platz 2
Lehrstuhl für Waldwachstumskunde
85354 Freising, Germany

More information about this series at <http://www.springer.com/series/124>

Francisco M. Cánovas • Ulrich Lüttge •
Rainer Matyssek • Hans Pretzsch
Editors

Progress in Botany Vol. 80

 Springer

Editors

Francisco M. Cánovas
Department of Molecular Biology
and Biochemistry
University of Málaga
Málaga, Spain

Ulrich Lüttge
Department of Biology
Technical University of Darmstadt
Darmstadt, Germany

Rainer Matyssek
Ecophysiology of Plants
School of Life Sciences Weihenstephan
Technical University of Munich
Freising, Bayern, Germany

Hans Pretzsch
Chair for Forest Growth and Yield Science
School of Life Sciences Weihenstephan
Technical University of Munich
Freising, Bayern, Germany

ISSN 0340-4773

ISSN 2197-8492 (electronic)

Progress in Botany

ISBN 978-3-030-10760-4

ISBN 978-3-030-10761-1 (eBook)

<https://doi.org/10.1007/978-3-030-10761-1>

Library of Congress Control Number: 2017959590

© Springer Nature Switzerland AG 2019

This work is subject to copyright. All rights are reserved by the Publisher, whether the whole or part of the material is concerned, specifically the rights of translation, reprinting, reuse of illustrations, recitation, broadcasting, reproduction on microfilms or in any other physical way, and transmission or information storage and retrieval, electronic adaptation, computer software, or by similar or dissimilar methodology now known or hereafter developed.

The use of general descriptive names, registered names, trademarks, service marks, etc. in this publication does not imply, even in the absence of a specific statement, that such names are exempt from the relevant protective laws and regulations and therefore free for general use.

The publisher, the authors, and the editors are safe to assume that the advice and information in this book are believed to be true and accurate at the date of publication. Neither the publisher nor the authors or the editors give a warranty, express or implied, with respect to the material contained herein or for any errors or omissions that may have been made. The publisher remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

This Springer imprint is published by the registered company Springer Nature Switzerland AG
The registered company address is: Gewerbestrasse 11, 6330 Cham, Switzerland

Contents

Vegetation, Climate and Soil: 50 Years of Global Ecology	1
Siegmar-W. Breckle	
Engineering Plants for the Future: Farming with Value-Added Harvest	65
Silvia Massa, Ombretta Presenti, and Eugenio Benvenuto	
Sequencing Plant Genomes	109
Daniel G. Peterson and Mark Arick II	
NAC Transcription Factors in Woody Plants	195
M ^a Belén Pascual, Fernando de la Torre, Rafael A. Cañas, Francisco M. Cánovas, and Concepción Ávila	
On the Elaborate Network of Thioredoxins in Higher Plants	223
Ina Thormählen, Belén Naranjo, José Abraham Trujillo-Hernandez, Jean-Philippe Reichheld, Francisco Javier Cejudo, and Peter Geigenberger	
From Aspartate to Ethylene: Central Role of N, C, and S Shuttles by Aminotransferases During Biosynthesis of a Major Plant Growth Hormone	253
E. Le Deunff	
Understanding the Factors Influencing Stem Form with Modelling Tools	295
Robert Schneider	
Northern Forest Trees Under Increasing Atmospheric Humidity	317
Elina Oksanen, Jenna Lihavainen, Markku Keinänen, Sarita Keski-Saari, Sari Kontunen-Soppela, Arne Sellin, and Anu Söber	

List of Contributors

Mark Arick II Institute for Genomics, Biocomputing & Biotechnology (IGBB), Mississippi State University, Mississippi State, MS, USA

Concepción Ávila Departamento de Biología Molecular y Bioquímica, Facultad de Ciencias, Universidad de Málaga, Campus Universitario de Teatinos, Málaga, Spain

Eugenio Benvenuto Department of Sustainability, Division of Biotechnology and Agroindustry, Laboratory of Biotechnology, ENEA - Italian National Agency for New Technologies, Energy and the Environment, Rome, Italy

Siegmar-W. Breckle Formerly Department of Plant Ecology, University of Bielefeld, Bielefeld, Germany

Rafael A. Cañas Departamento de Biología Molecular y Bioquímica, Facultad de Ciencias, Universidad de Málaga, Campus Universitario de Teatinos, Málaga, Spain

Francisco M. Cánovas Department of Molecular Biology and Biochemistry, University of Málaga, Málaga, Spain

Francisco Javier Cejudo Instituto de Bioquímica Vegetal y Fotosíntesis, Universidad de Sevilla and CSIC, Sevilla, Spain

Fernando de la Torre Departamento de Biología Molecular y Bioquímica, Facultad de Ciencias, Universidad de Málaga, Campus Universitario de Teatinos, Málaga, Spain

Peter Geigenberger Fakultät für Biologie – Pflanzenmetabolismus, Ludwig-Maximilians-Universität München, Munich, Germany

Markku Keinänen Department of Environmental and Biological Sciences, University of Eastern Finland, Joensuu, Finland

Sarita Keski-Saari Department of Environmental and Biological Sciences, University of Eastern Finland, Joensuu, Finland

Sari Kontunen-Soppela Department of Environmental and Biological Sciences, University of Eastern Finland, Joensuu, Finland

E. Le Deunff Normandie Université, UNICAEN, ICORE, Caen, France

Jenna Lihavainen Department of Environmental and Biological Sciences, University of Eastern Finland, Joensuu, Finland

Silvia Massa Department of Sustainability, Division of Biotechnology and Agroindustry, Laboratory of Biotechnology, ENEA - Italian National Agency for New Technologies, Energy and the Environment, Rome, Italy

Belén Naranjo Fakultät für Biologie – Molekularbiologie der Pflanzen, Ludwig-Maximilians-Universität München, Munich, Germany

Elna Oksanen Department of Environmental and Biological Sciences, University of Eastern Finland, Joensuu, Finland

M^a Belén Pascual Departamento de Biología Molecular y Bioquímica, Facultad de Ciencias, Universidad de Málaga, Campus Universitario de Teatinos, Málaga, Spain

Daniel G. Peterson Institute for Genomics, Biocomputing & Biotechnology (IGBB), Mississippi State University, Mississippi State, MS, USA

Ombretta Presenti Department of Sustainability, Division of Biotechnology and Agroindustry, Laboratory of Biotechnology, ENEA - Italian National Agency for New Technologies, Energy and the Environment, Rome, Italy

Jean-Philippe Reichheld Laboratoire Génome et Développement des Plantes, Université de Perpignan Via Domitia, Perpignan, France

Laboratoire Génome et Développement des Plantes, Centre National de la Recherche Scientifique, Paris, France

Robert Schneider Chaire de recherche sur la forêt habitée, Département de Biologie, Université du Québec à Rimouski, Rimouski, QC, Canada

Arne Sellin Institute of Ecology and Earth Sciences, University of Tartu, Tartu, Estonia

Anu Sõber Institute of Ecology and Earth Sciences, University of Tartu, Tartu, Estonia

Ina Thormählen Fakultät für Biologie – Pflanzenmetabolismus, Ludwig-Maximilians-Universität München, Munich, Germany

José Abraham Trujillo-Hernandez Laboratoire Génome et Développement des Plantes, Université de Perpignan Via Domitia, Perpignan, France

Laboratoire Génome et Développement des Plantes, Centre National de la Recherche Scientifique, Paris, France

Curriculum Vitae



Siegmund-W. Breckle born on 27 February 1938 in Stuttgart, studied chemistry, biology, geology and geography at Stuttgart, Innsbruck and Hohenheim. In 1966 he got his Dr. rer. nat. with a dissertation on the ecology of *Quercus suber* in Catalunya (with HEINRICH WALTER) at the University of Hohenheim. After 3 years as a lecturer at the Faculty of Science, University of Kabul/Afghanistan he was Assistant Professor at the Institute of Pharmaceutical Biology at the University of Bonn. After his habilitation in 1976 (halophyte ecology in Utah/USA), he became Associate Professor in Bonn. At the same time, he had a guest lecturer-ship at the University of Marburg. In 1979, he was appointed Professor and Head of the Department of Ecology at the new University of Bielefeld. After retiring in 2003, he was guest professor at the University of Utsunomiya/Japan. His scientific interests are plant ecology and geo-botany, vegetation and stress ecology. Projects in deserts (Negev, Namib, Aralkum) and in tropical mountain rain forests (Costa Rica, Ecuador) were

carried out in close co-operation with colleagues in the host countries. The projects were funded by DFG (German Research Foundation), BMBF (German Ministry of Education and Research), BMBL (German Ministry of Agriculture), DAAD (German Academic Exchange Service), VW-Foundation, Schimper-Foundation, Alexander-von-Humboldt Foundation and the University of Bielefeld. His publication record lists more than 300 papers, as well as publication, edition and co-edition of many scientific books. He served the Faculty as Academic Dean in 1984–1995 and from 1990 to 2003 he was responsible for the environmental council of the University of Bielefeld. He supervised many doctoral theses (c. 20), diploma theses (c. 130) and teachers' examination (c. 25). He was an external examiner at the University of Cairo/Egypt, Aswan/Egypt, Karachi/Pakistan, Tel Aviv/Israel, Coimbra/Portugal and Vienna/Austria. He served as examiner in many evaluation panels and on editorial boards of scientific journals. He founded four affiliation treaties of the Faculty of Biology/University of Bielefeld, with the University of Coimbra, with the Live Science Department at Tel Aviv University, with the Jardín Botánico Nacional at Santo Domingo/Dominican Republic and with the Sede Occidente in San Ramón/University of Costa Rica. For more than 10 years, he was speaker of the Afghanistan Research Group; he is, to date, vice president of the Swiss Afghanistan Foundation and the Schimper-Foundation (Stuttgart-Hohenheim). He is a member of the Academy of Science and Arts Peter I. St. Petersburg. *Astragalus brecklei* I. Deml, *Acantholimon brecklei* Rech. f. & Schiman-Czeika and *Anemone X brecklei* Rech. fil. were named after collections in his herbarium; some 15–20 new species and subspecies were described from his Afghan specimens.

Vegetation, Climate and Soil: 50 Years of Global Ecology



Siegmar-W. Breckle

Contents

1	Introductory Remarks and Early Background at Stuttgart, Innsbruck, Hohenheim, Kabul, Bonn, Logan (Utah) and Bielefeld	2
2	Halophytes and Salinity	8
3	Heavy Metals, Root Growth and Forest Dieback	14
4	High Mountains and Altitudinal Stress	17
5	Desert Ecology	20
	5.1 Negev (Nizzana Sand Dunes)	21
	5.2 Aralkum (The Desiccated Sea Floor)	25
6	Tropical Ecology, Canopy Structure and Growth Dynamics	30
	6.1 Costa Rica	30
	6.2 Ecuador	38
7	Wealth of Biodiversity	41
	7.1 Tropics	41
	7.2 Afghanistan	43
8	Ecosystems of the Earth	47
9	Applied Biology and Ecology	48
10	Teaching	49
11	Some Final Remarks	51
	References	54

Abstract In this essay, more than 50 years of studies on a broad spectrum of ecological topics is reviewed. Many research questions in desert ecology, in tropical ecology and in stress ecophysiology were studied, mainly in the field but often completed by analysis in the lab.

To keep in mind the complexity of ecological systems, it was necessary to go into detail with very specific approaches but always keeping in mind a synthetic view. More and more it became clear that the biodiversity in many ecosystems plays an important role for the future. Vegetation, climate and soil are interwoven in

Communicated by Ulrich Lüttge

S.-W. Breckle (✉)

Formerly Department of Plant Ecology, University of Bielefeld, Bielefeld, Germany

e-mail: sbreckle@gmx.de

ecosystems; the rapid developments in science – as well as the fast development of methods, techniques and data pools – are a big challenge. Many aspects of global ecology have been studied in the last 50 years. Some examples are demonstrated here. This essay will remain a rather historical treatise. It will give examples of experimental and field work. It will be a look back with great gratitude on what was able to be achieved and experienced.

1 Introductory Remarks and Early Background at Stuttgart, Innsbruck, Hohenheim, Kabul, Bonn, Logan (Utah) and Bielefeld

The following review gives a personal overview of some of the scientific topics tackled over the last 50 years and characterizes a somewhat unusual career, which asked many questions on many very different ecological topics. The scientific depth was sometimes limited, and the scientific breadth was immense and always satisfying.

Breadth or depth? I always have had the feeling that, as a scientist, I was lucky not to do research for 25 or 40 years on *Sinapis* seedlings or on one gene of *Arabidopsis*, although it is certainly very important too.

I had the privilege to study three subjects at the University (Technische Hochschule) of Stuttgart (chemistry, biology and geology) for my teacher's exam. Later, geology had to be replaced by geography. But ethnology, astrophysics, engineering, philosophy or even Beethoven piano sonatas could come into lectures. This was fascinating, as was studying for 1 year at the University of Innsbruck with a touch of high mountain ecology. After two obligatory practical courses at schools (each for 4 weeks), the three classes in chemistry were so different that even the teacher had problems in keeping the classes on the same parallel level.

The thesis for the 1963 teacher's exam was in inorganic chemistry at Stuttgart (supervised by Joseph Goubeau). The title was "Preparation of a Compound Between Perchloric Acid and Hydrogen Peroxide" (Breckle 1963). Those who know chemistry would judge that this has something to do with rocket explosives. The questions were: How stable is the ionic compound? Is a salt existent that could be called "perhydronium perchlorate"? (Fig. 1). In fact, this is a very explosive salt, only stable below -50°C . By infrared and Raman spectroscopy, the cohesive force and the bond angles could be calculated. However, the monocrystalline sodium chloride (NaCl) cuvette, after several tests, exploded once, and all of the windows of the lab – and also, for some days, my auditory sense and hearing – were damaged. Thus I started writing the thesis and finished my teacher's studies in 1963 with the state examination (inorganic and organic chemistry, zoology, botany, geography and the Philosophicum).

Then I switched back to botany, my old hobby. Instead of becoming a teacher or having a well-paid job at one of the large chemical companies (Bayer, BASF), I preferred to tackle the question: What are the competitive conditions between

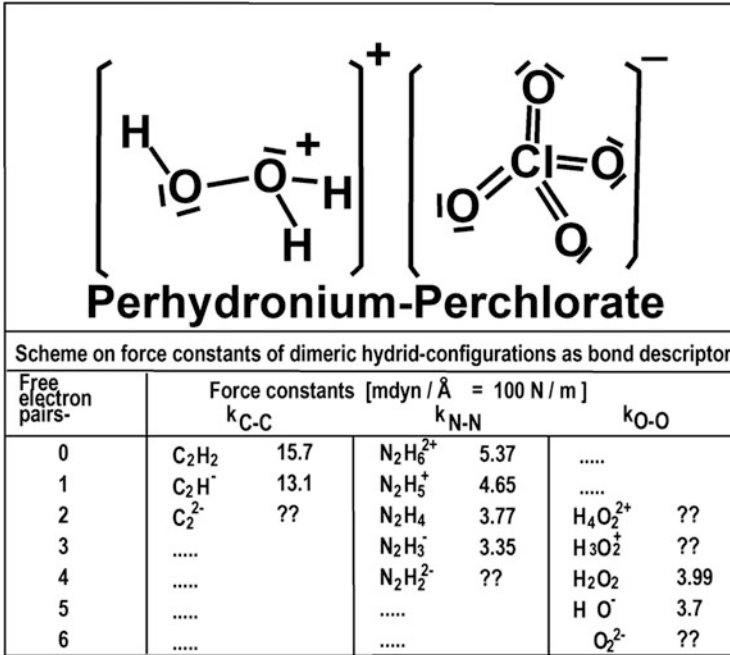


Fig. 1 Structure of perhydronium perchlorate and scheme of force constants of dimeric hydrid configurations as a bond descriptor (Breckle 1963)

Quercus suber and *Quercus ilex* in Catalunya in north-eastern Spain? From the University of Hohenheim with an old Volkswagen Beetle and a 1,000 DM fellowship from the Carlos Faust Foundation in Barcelona – the only external funding – I started at the famous Mar I Murta Botanical Garden in Blanes, where they wanted me at once as a gardener! Advice came by letters from my supervisor, Heinrich Walter, in South America, where he was on his sabbatical. It turned out that the cork oak, *Quercus suber*, uses twice as much water as *Quercus ilex* (Fig. 2), with a very large root system (Breckle 1966). And, growing in Germany, young trees of *Quercus suber* were more frost resistant than those of *Quercus ilex* – in contrast to many observations in Spain or in Italy at Lake Maggiore (Sakai and Larcher 1987).

There was some pressure to publish the work, since Heinrich Walter was near retirement. On the other hand, a doctoral thesis at that time was acknowledged as a publication providing more details than a publication in a journal, as Beck (2017) also indicated, and a cumulative dissertation was not known or allowed at that time. The Rigorosum (viva) at the University of Stuttgart-Hohenheim was very comprehensive (one long oral of 90 min), covering botany, ecology and seed science.

My studies at Stuttgart and Hohenheim were a very helpful basis for future research. Teaching at the Chemieschule and during practicals and field trips around Hohenheim made me learn much about plants, their behaviour and ecology. Behind that were chemistry and chemical reactions and pathways. But doing studies and

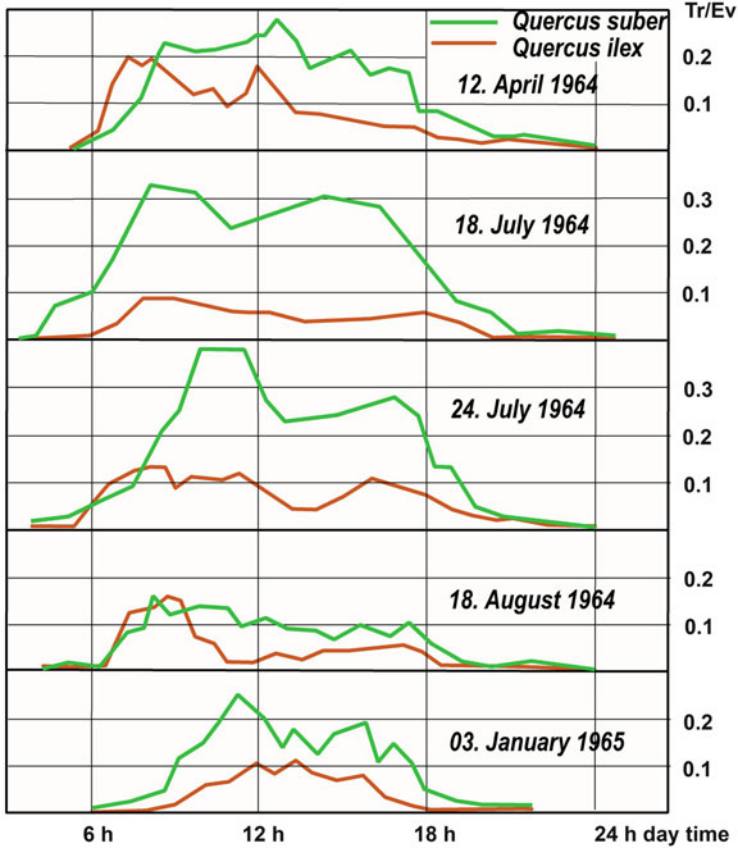


Fig. 2 Daily courses of the transpiration-to-evaporation ratio of *Quercus suber* and *Quercus ilex* in Catalunya (Breckle 1966)

measurements in nature proved to be more complicated; it took many replications to understand diurnal and annual fluctuations.

Parallel to my stays in north-eastern Spain, Helmut Freitag used his Carlos Faust Fellowship for research in the semi-desertic south-eastern Spain. He once mentioned to me the affiliation between the universities of Bonn and Kabul and that there was an existing German team of lecturers in Kabul at its Faculty of Science. We tried and then succeeded in getting a new job in Afghanistan – for us an unknown country. After Freitag's habilitation and my doctorate, we started at the end of 1966 to build up a curriculum for botany, giving lectures, courses, seminars and excursions, jointly for male *and* female students at the Faculty of Science, Kabul. Uta Breckle organized the lab work and the establishment of a herbarium.

Again, there were high mountains. During the summer vacation, when all of the steppe and semi-deserts in the lowlands were dry and arid, the Hindu Kush was an ideal place. One of the many highlights was an expedition to the Wakhan (Fig. 3a),

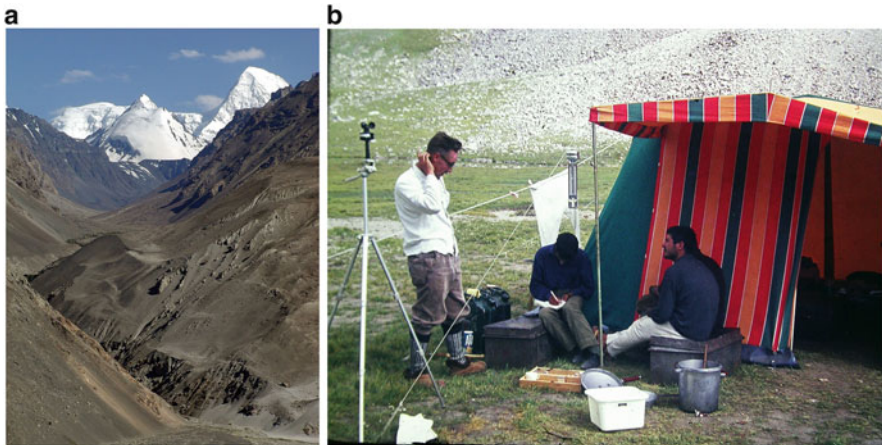


Fig. 3 (a) Nushaq (7,492 m), the highest peak in Afghanistan, in the eastern Hindu Kush, near Qazi Deh, Wakhan (photo courtesy of C. Naumann, 2002). (b) Base camp at Kotale-Wazit (4,620 m) for microclimatic measurements; data collecting and evaluations with Afghan counterparts (photo courtesy of P. Schneider, August 1968)

with the permission of the Afghan King Mohammad Zahir Shah (deposed in 1973); in August 1968 we spent 1 month in the Wazit area (at an altitude of 4,600 m) as our base camp. Some microclimatic measurements (Fig. 4), not repeatable until now – indicating the specific high-altitude conditions, vegetation surveys and many herbarium collections, etc. – were made (Breckle 1973). Advanced Afghan students who later got fellowships to study in Germany were involved (Fig. 3b).

Other mountain ranges (Koh-e Baba, Safed Koh, etc.) were studied up to the nival region (Breckle 1975; Breckle and Frey 1974, 1976). The number of vascular plants known from above 5,000 m increased from 12 to 40 species. Decades later, many of the data and the photographs (see Sect. 7.2) were used for inventories.

As a member of the German team within the affiliation between Bonn University and the University of Kabul, I had the opportunity to start as an assistant at the Institute of Pharmaceutical Botany at the University of Bonn; the first textbook for students was published in 1978 (Kating and Breckle 1978) and the eighth edition came out in 2014 (Leistner and Breckle 2014).

In Afghanistan, it was very obvious that in dry areas the role of halophytic plant species is very important in many different vegetation types. Evaluation of material and data from Afghanistan, as well as a project comparing two competing halophytic species in the Great Salt Lake area and at the Utah State University in Logan, finally led to my habilitation (Breckle 1976). The question was: Do recreting halophytes have an advantage in the salt desert of Utah, and under what conditions? Mainly, ecophysiological responses of *Atriplex confertifolia* (C_4) and *Ceratoides lanata* (C_3) were compared, and later in Germany cultivation experiments were performed. Sodium (Na) turnover on both sites was calculated from respective analytical data (Fig. 5). *Atriplex confertifolia* exhibited a much higher turnover by litter and salt

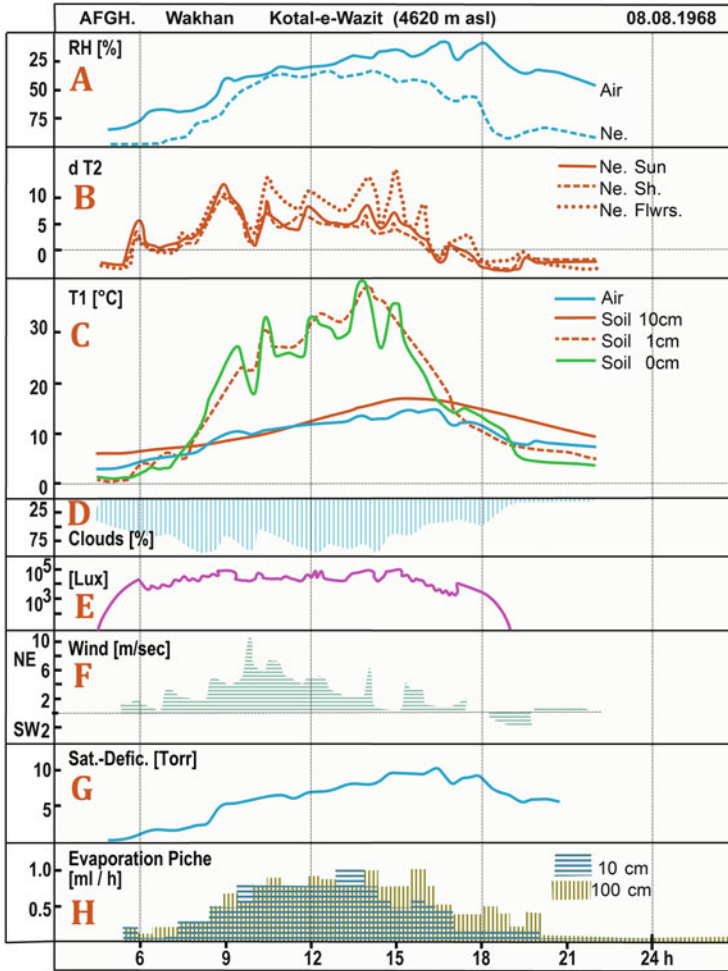


Fig. 4 Daily courses (measured on 8 August 1968) of some microclimatic and ecophysiological parameters at an alpine site at Kotale-Wazit (Wazit pass, 4,620 m; Wakhan) (Breckle 1973). (a) Relative humidity (air, 1.5 m; Ne, between *Nepeta pamirensis* [10 cm]). (b) Temperature difference (K) to air temperature of *Nepeta* sun leaves, shade leaves and flowers. (c) Air temperature (1.5 m) and soil temperatures (surface, 1 cm, 10 cm depth). (d) Cloudiness (% of whole sky). (e) Radiation (lux). (f) Wind speed (north-east or south-west). (g) Saturation deficit of air (torr). (h) Evaporation (Piche 3 cm) (ml h^{-1}), 10 and 100 cm

bladder hairs than *Ceratoides*, which, however, had a rather high salt content in its roots. Salt is accumulated in the roots of *Ceratoides*; in *Atriplex*, it is in the shoot. The dominant species of the salt deserts are shown in Fig. 6, according to their ecological requirements.

In Nov. 1979, I went to Bielefeld and started to establish the new Department of Plant Ecology. Together with a small team (some co-workers and a technician who came from Bonn), we had plenty of room but almost no equipment at the new

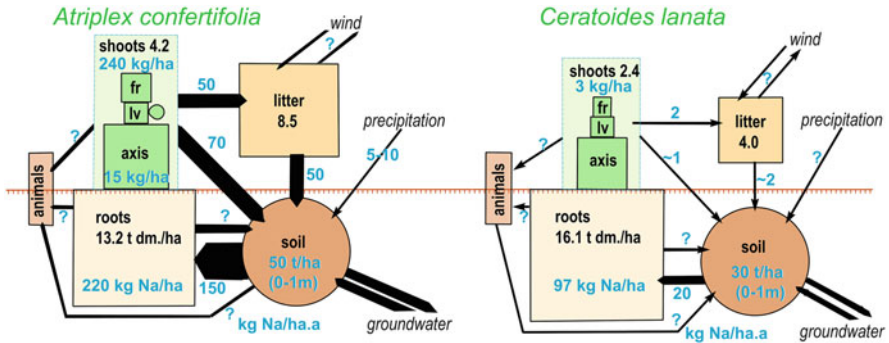


Fig. 5 Estimated sodium (Na^+) turnover ($\text{kg ha}^{-1} \text{a}^{-1}$) (blue figures) at the *Atriplex confertifolia* site (left) and at the *Ceratoides lanata* site (right) in the Curlew Valley, Utah; compartmental storage amount of sodium (kg ha^{-1}) and biomass (black figures) (total dry mass [tdm] ha^{-1}) (Breckle 1976)

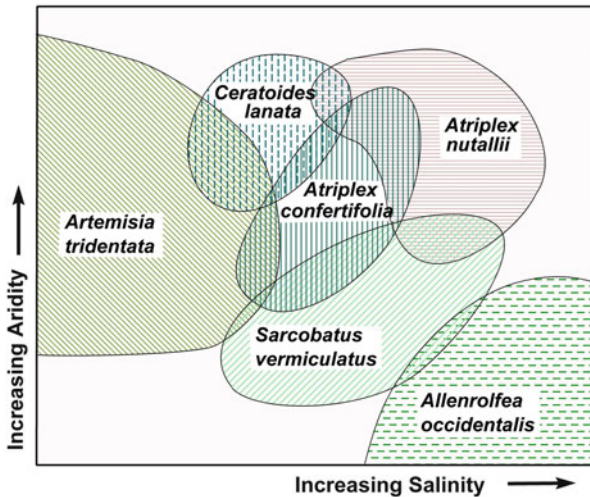


Fig. 6 Aridity/salinity ecogram of the main dominant species in the Great Salt Lake area, Utah (Breckle 1976)

university. Much new material had to be purchased; teaching started with new lectures, seminars, practical lab and field courses, and excursions.

Most of the first studies in Bielefeld had an autecological basis and focused on the effect of plants on distinct stress factors such as salt or heavy metals. Synecology, geobotany and vegetation surveys were later included in several research projects.

During the following years in Bielefeld, many projects and studies were undertaken in various countries abroad. Many candidates asked for a thesis, but we could not take all. We were able to publish some of the results in *Bielefelder Ökologische Beiträge* (BÖB), starting with volume 1 in 1985. After I became a pensioner in 2003, regular editions stopped with volume 20 in 2004, but volume 21 was published in 2017.

2 Halophytes and Salinity

Halophytic research in Afghanistan (1976) and Iran (1977) mainly focused on the question of mineral ion uptake and expression of phenotypes in the various halophytic taxa. The main types (Henkel and Shakhov 1945; Walter 1961) were defined according to salt uptake (Fig. 7), and their occurrence along salt gradients turned out

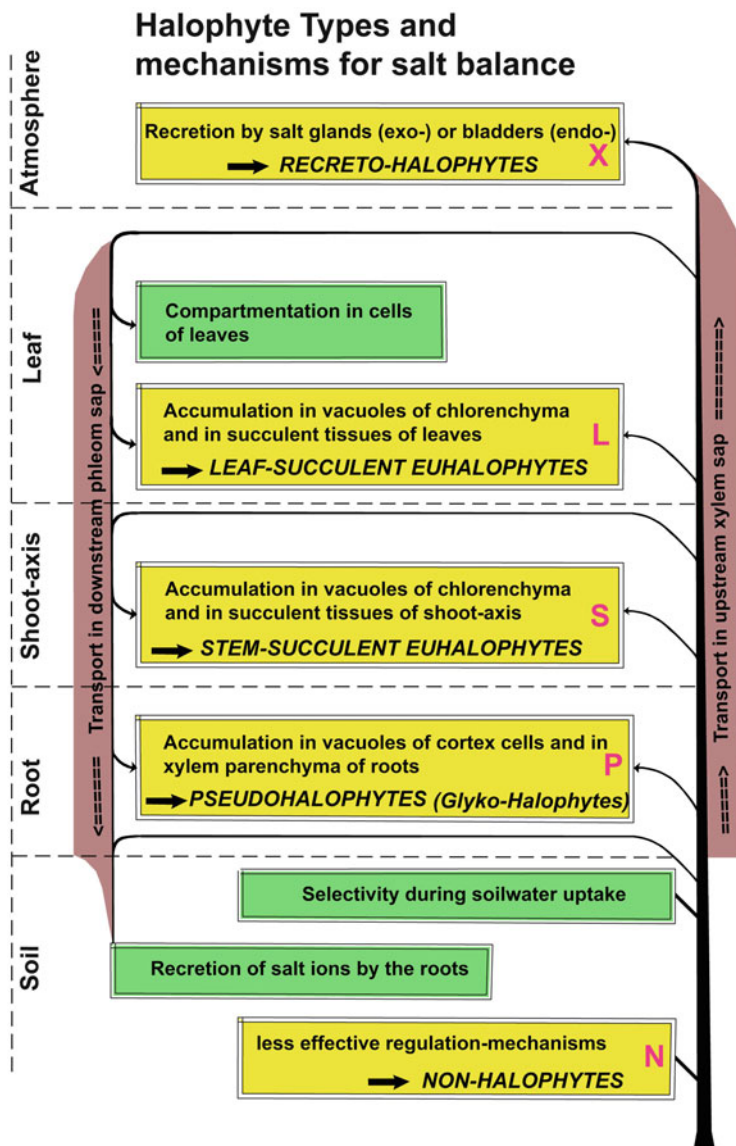
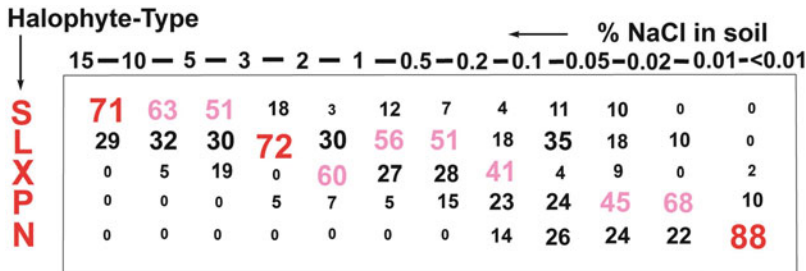


Fig. 7 Main halophyte types and applied mechanisms of salt balance in higher plants (Breckle 1976)



Abundance of halophyte types (percentages) along a salinity gradient

Fig. 8 Percentage values of calculated abundances of halophytic plant types (S, L, X, P, N; see Fig. 7) arranged according to the salinity gradient (logarithmic intervals) averaged from eight halophytic zonation in Iran and Afghanistan (Breckle 1986)

to be rather similar at many saline sites. The most salt tolerant are in general the stem-succulent halophytes (Fig. 8), often performing C₄ photosynthesis.

Already in Bonn, one of my first candidates had proved the salt tolerance of whole plants in comparison with tissue cultures in *Phaseolus* and *Suaeda* (Hedenström and Breckle 1974). The big difference that young intact plants exhibit is not mirrored in tissue cultures. To be a successful halophyte requires an intact complex network of storage space and transport systems.

Along ocean coasts, the quality of seawater is rather identical, with about 3.5% NaCl. Other ions such as potassium (K⁺) or magnesium (Mg²⁺) have only low concentrations. Coastal halophytes have thus evolved some kind of salt tolerance by different means. The dominant ecophysiological factor NaCl modifies many processes at all ecological and physiological levels (Fig. 9). It is an excellent example of how many biological processes are interwoven at the various levels of complexity (Breckle 2002a).

In arid desert regions, in contrast to saline coastal areas, the potential evaporation exceeds the water input by precipitation and thus enrichment of various soluble ions takes place (Breckle 2002b). The chemistry is more varied; the pH can be very alkaline, and sulphate (SO₄²⁻) or bicarbonate (HCO₃⁻) can be accumulated. Sometimes K⁺ or Mg²⁺ or lithium (Li⁺) is enriched. The uptake of those ions is often very specific for different species (thus physiotypes can be defined) (Albert 2005).

Studies on the ecology of halophytes were also done by several of my students over many years. The sodium-to-potassium (Na:K) ratio (Fig. 10), as well as the storage of anions and cations, showed great differences between species (Fig. 11). This has been shown for Iranian halophytes too (Matinzadeh et al. 2013).

In recreted halophytes such as *Limonium* species, one can distinguish between two processes for selecting ions: one is the discrimination of ions by the transport process from the root to the leaf, and the other from the leaves to the salt glands (Fig. 12). Obviously, other species behave rather differently (Wiehe 1986; Wiehe and Breckle 1990).

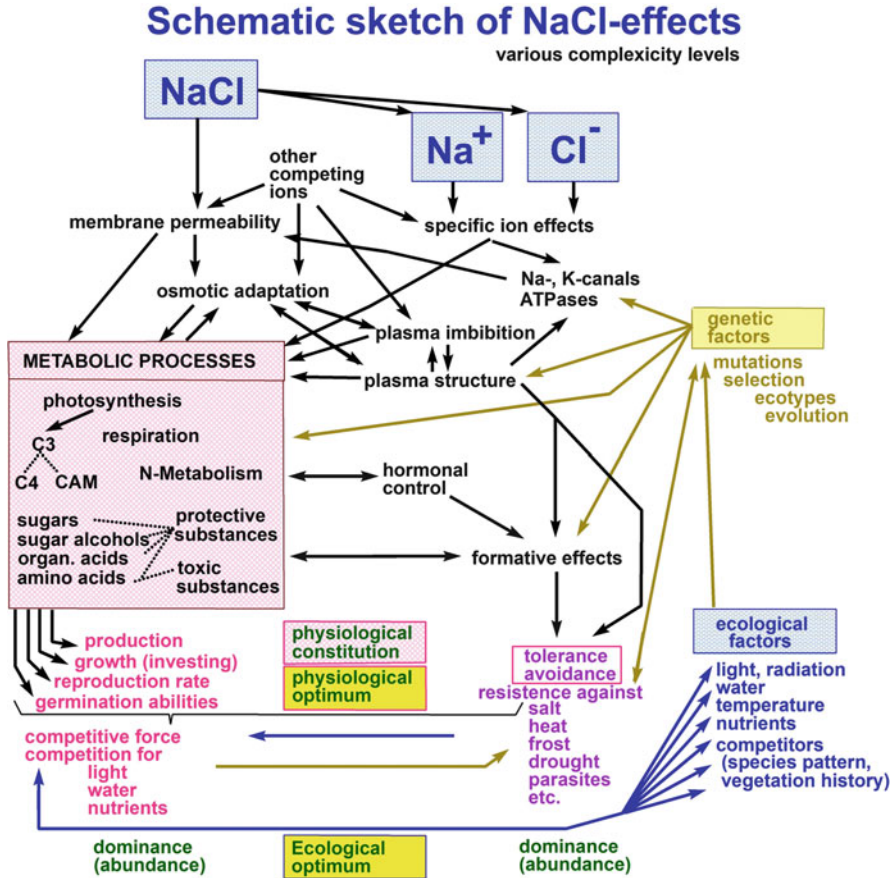


Fig. 9 Scheme of sodium chloride (NaCl) effects on plants at various complexity levels between genetic and ecological factors (Breckle 2005a)

In recreting halophytes such as *Atriplex*, only a few strongly halophytic species exhibit intensive NaCl turnover by bladders (Jones 1970; Lüttge 1971, 2016; Waisel 1972; Breckle 2002a; Osmond 1974; Reimann and Breckle 1988; Schirmer and Breckle 1982). The ratio of total bladder volume to leaf lamina volume in *Atriplex confertifolia* in very young leaves is above 2, keeping young growing tissues low in salt content; with ageing, it declines to about 0.4, and the bladders start to shrink or are blown away, thus eliminating NaCl from the leaves (Breckle 1976). In particular, *Atriplex* was studied very intensively (Tiedemann et al. 1984). Yuan et al. (2016) reported on how recretion in recreto-halophytes may occur. But salt tolerance and the genetic background in halophytes are still not really understood (Song and Wang 2015). Despite major efforts in analysing single genes responsible for salinity tolerance, some old questions (Breckle 1990, 1995) are still unresolved.

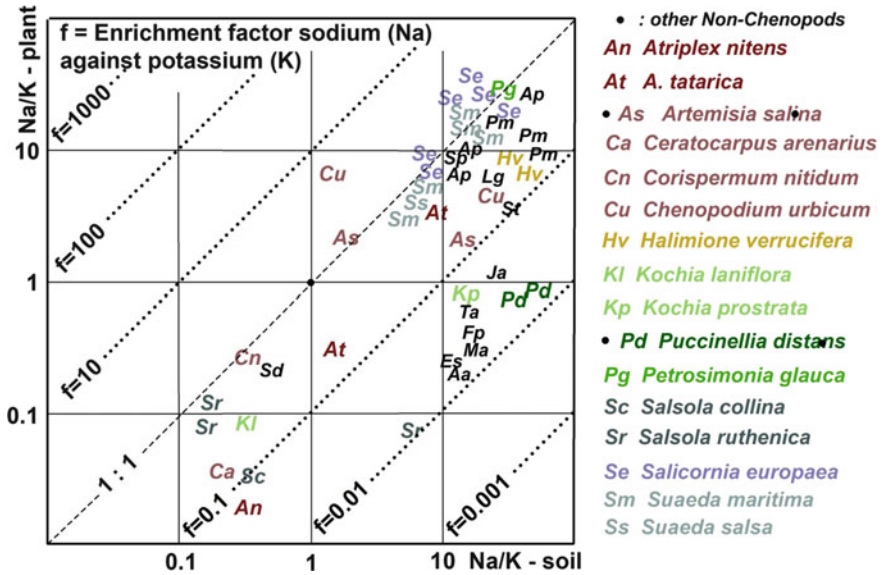


Fig. 10 The sodium-to-potassium (Na:K) ratio in soil is not mirrored in plants (Mirazai and Breckle 1978)

Roots of plants – the invisible half – have also been studied. In collaboration with Yoav Waisel from Tel Aviv [author of volumes on *Plant Roots: the Hidden Half* (Waisel et al. 1991, 1996, 2002; Eshel and Beekman 2013)], some methods with hydroponics and aeroponics have been tested (Waisel and Breckle 1987). The question was: How do roots behave under salt stress? Large aeroponic chambers (Breckle et al. 2001a), more than 2 m high, were constructed in a new greenhouse in Bielefeld, similar to the Racine lab in Tel Aviv. Yoav Waisel stayed very often with us in Bielefeld. The sophisticated technique for keeping a constant pH and constant temperature of the nutrient solution could be managed for a period of several weeks. Tomato plants grown under different salt stress developed huge root systems in Bielefeld, as well as in Tel Aviv (Fig. 13); cutting of 90% of the roots did not have any effect on the transpiration of the upper plant parts. The architecture of root systems is very adaptive; the ratio of primary and secondary roots exhibits a strong shift to secondary roots with salt stress (Fig. 14). Field studies with mini-rhizotrons (glass tubes of 5 cm diameter) and TV cameras on roots of desert plants in the Negev Desert gave interesting results, but evaluation with automatic processing software is still not sufficiently resolved (Breckle et al. 2001c; Erz et al. 2005; Veste et al. 2005). It is a challenge for all root studies.

An interesting example of salinity effects was studied in the parasitic *Loranthus* growing on various halophytic hosts (Todt et al. 2000). In the southern Arava Valley (Negev Desert), *L. acaciae* was checked on five halophytic and ten non-halophytic host plants. Water content and succulence of mistletoes increased on halophytic

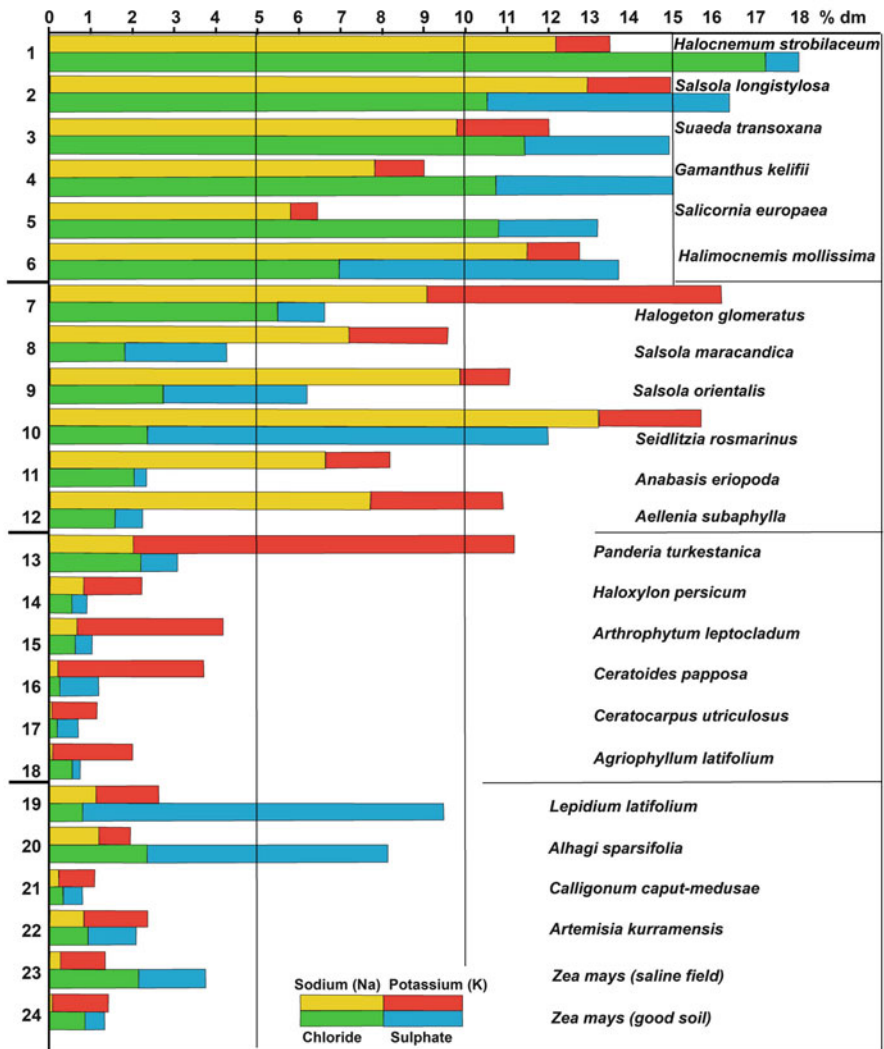


Fig. 11 Ion content in various halophytic and non-halophytic species from northern Afghanistan (after Mirazai and Breckle 1978)

hosts, and the leaf volume increased four to five times in comparison with those on non-halophytic hosts exhibiting typical halo-succulence. It behaves like a typical facultative eu-halophyte (Veste et al. 2014).

Of the world’s land surface area, at least 6% is salt-affected land (Flowers and Yeo 1995; Munns 2005). Large areas in drylands and along coasts are naturally salt affected (Breckle 2002c), but with irrigation under arid climatic conditions, secondary salinization (Breckle 1989) is a big threat. Since the work of Boyko (1966), and then Waisel (1972) and Gallagher (1985), the use of seawater for agriculture has very

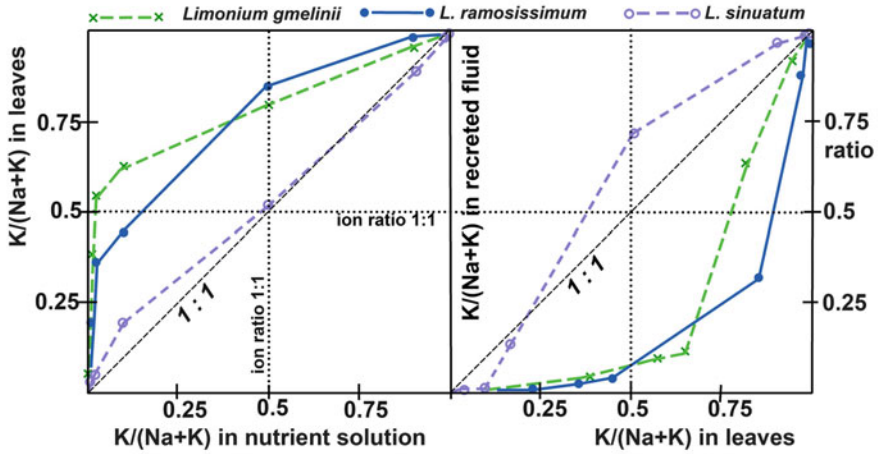


Fig. 12 Potassium-to-alkali ion ratio in leaves and in recreted fluid in three *Limonium* species under different salinities (Wiehe 1986; Wiehe and Breckle 1990)



Fig. 13 Tomato roots grown in aeroponic chambers in the root lab of the Tel Aviv Botanical Garden (photo: S. W. Breckle, 1997) (photo: S. W. Breckle)

often been discussed and studied. But despite intensive research and many projects, only a few organisms have been found that can be grown with seawater. Thus the question was asked: How can we grow plants with seawater? (Breckle 2009). Full-strength seawater can be used to sustainably irrigate only a few special plants, e.g. *Sesuvium*, *Aster*, *Salicornia* (Ventura and Sagi 2013) – maybe now that *Salicornia* salad is becoming quite popular – and *Spartina* along sandy seashores, without impairing soil quality provided that sufficient drainage exists. Intensive agriculture with seawater with high production per surface area is utopian. It was

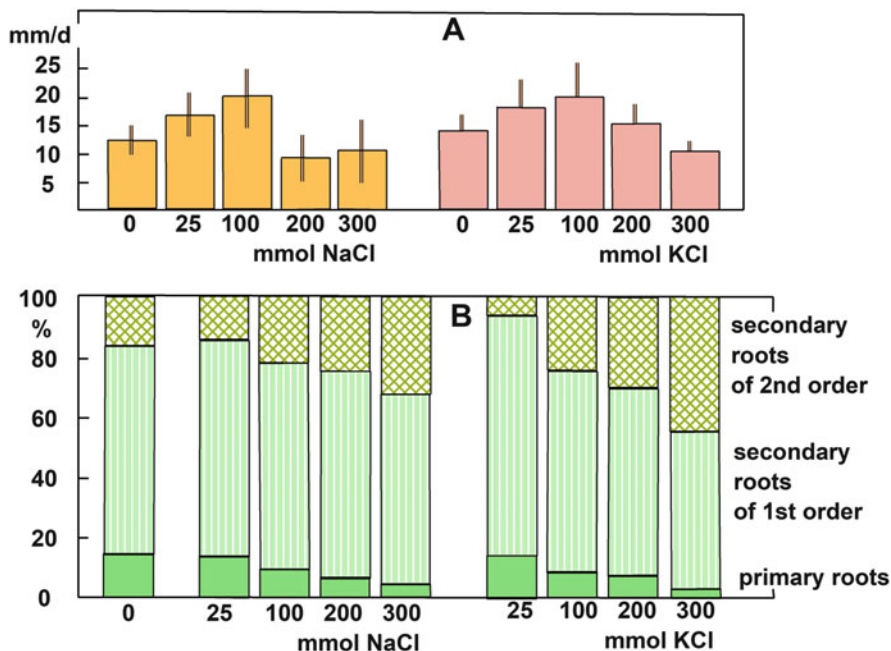


Fig. 14 Root structure of *Chenopodium album* under different salinities of sodium chloride (NaCl) and potassium chloride (KCl) treatments. (a) Mean daily growth of main root (mm per day). (b) Ratios of lengths of primary and secondary roots after 22 days (Seidel 1988; Breckle 1996b)

often said that greening of deserts, using halophytes, could partially help increase the biomass on the land surface and thus reduce global warming. But it would be much wiser to stop further deforestation in all of the humid climatic zones, especially in the tropics and in the Siberian and Canadian taiga, and to let all secondary forests grow, instead of transforming them from highly biodiverse primary forests into poor McDonald’s beef sources (Breckle 2009). Additional costs to maintain sustainable irrigation and leaching systems to keep the salinity of the soil low pay more in the long run. The take-home message “no irrigation without drainage” means that it pays more to invest in desalination systems. This is especially important under very dry climatic conditions (Breckle et al. 2003) and when using urban water, as is done in southern Israel in the Yotvata farming area with brackish sewage water from Eilat.

3 Heavy Metals, Root Growth and Forest Dieback

Stress in plants is not only a result of salinity; many other factors cause stress. One is heavy metals. One of the first studies on lead (Pb) effects started in Bonn; along highways, the accumulation of Pb was checked (Lerche and Breckle 1975). When do trace metals have a measurable effect on the ecological behaviour of plants and

trees? Along German highways, the Pb content in and on leaves exceeded the background content in the adjacent forests by 20–40 times. Later, we checked the accumulation of Pb, cadmium (Cd), zinc (Zn) and nickel (Ni) in the annual rings of beech and fir trees; it revealed a rather complex picture. The distribution of heavy metals in annual rings does not give a retrospective picture of the heavy metal stress over time. The physiological mobility of heavy metals within wood along radial pathways in most cases manifested in maximum concentrations of Pb and Cd along the sapwood–heartwood border and the lowest concentrations in the outermost rings, near the cambium (Hagemeyer and Breckle 1986; Hagemeyer et al. 1993; Brackhage et al. 1996). The findings were similar for potassium (K) and calcium (Ca), in contrast to Mg, Ni and Zn, for which the concentrations were lowest at the sapwood–heartwood transition. But both the distribution pattern and the concentrations of minerals in trunk wood were subject to seasonal variations.

Root growth is very sensitive to heavy metals. Reduced root growth, however, can be even overcompensated for when roots reach soil layers with low concentrations (control soil) (Weisser et al. 1990, Fig. 15). There, artificially enriched horizons in root boxes turned out to be very useful. Later also mini-rhizotrons (see Sect. 5.1) were found to be very suitable for experimental sets.

In many papers (Breckle and Kahle 1992; Kahle and Breckle 1992; Breckle 1996a, b), the effects of Pb and Cd on beech were shown. In the early 1900s, there

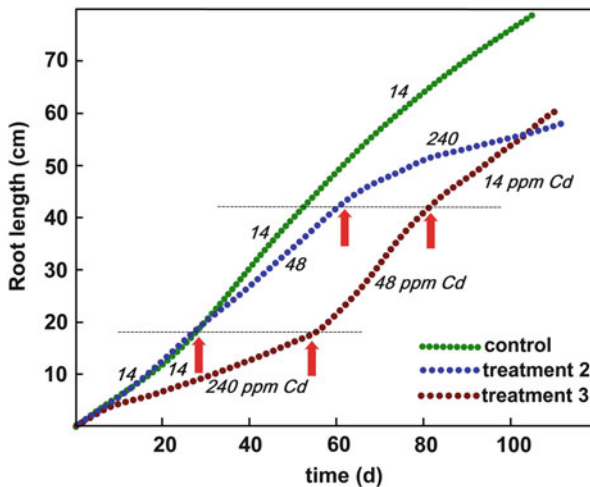


Fig. 15 Root length growth of beech seedlings in root chambers within 3 months. The root chambers were filled with three horizons of soil, differing in heavy metal content: *green*, all three horizons with low cadmium (Cd) (14 ppm); *blue*, increasing Cd content, lower 14, middle 48, upper horizon 240 ppm Cd; *brown*, decreasing Cd content, lower 240, middle 48, upper 14 ppm Cd. *Red arrows* indicate horizon limits (Weisser et al. 1990; Breckle and Kahle 1992; Hagemeyer and Breckle 1996)

was much research on forest dieback, especially in spruce. We started with beech. Later it became clear that deciduous trees also exhibited distinct signs of stress, with lowered soil pH, soluble aluminium (Al) in soil, and ozone (O₃) on leaves. With young beech saplings, it could be shown that in a rather short time of Cd stress, transpiration rates were much reduced (Hagemeyer et al. 1986, Fig. 16).

Only slight synergistic effects of Pb and Cd in beech saplings could be detected (Bertels et al. 1989). Changes in uptake of essential elements were, however, obvious but strongly dependent on soil pH (Kahle et al. 1989a, b). Mg and Ca uptake was antagonistic to Cd uptake, but this was not so with Pb. In general, it became obvious that the concentrations of Pb in exposed acid forest soils in Central Europe were sufficiently high to affect the germination and growth of saplings of beech. The “critical concentrations” could be defined as about 2 ppm of Cd and 25 ppm of Pb (1 N NH₄-acetate extractable fraction, pH 7). The reduction of wood formation seen with heavy metal contamination was distinct in some places of North Rhine–Westphalia (Lammersdorf, Stolberg), causing economic losses (Breckle and Hagemeyer 1992).

Fig. 16 Rapid effect of cadmium (Cd) stress on transpiration rates ($\text{mg h}^{-1} \text{cm}^{-2}$) of 2-year-old beech saplings (*Fagus sylvatica*) cultivated in nutrient solution, with indication of the least significant difference (LSD) of 90% (Hagemeyer et al. 1986)

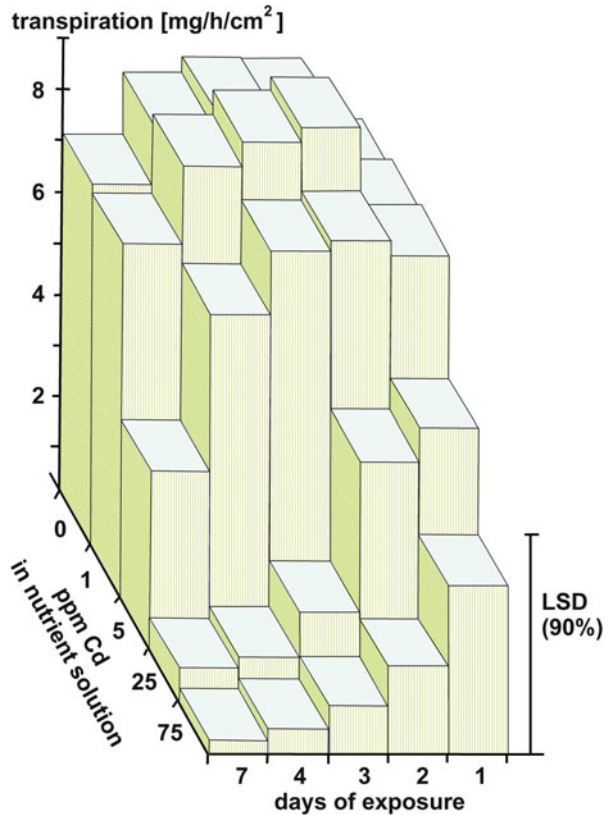


Fig. 17 *Viola guestphalica* (the blue calamine violet) – the only endemic plant of Westphalia – at the Bleikuhle near Blankenrode (photo: S. W. Breckle)



Metallophytes – plants that are able to withstand high levels of heavy metals in the soil – often accumulate heavy metals in the plant body (Breckle 1997b). They are often very specific and very rare (Fig. 17). As with the idea of desalinating soils by halophytes (Breckle 2009), quite often one finds papers discussing the idea of decontaminating soils containing heavy metals. By simply calculating realistic turnover rates, we often disillusion people, since the desalination times are about 50–500 years; the times required for decontamination of heavy metals (Pb, Cd and Zn) are in the same range. Another purpose would be to use plants for mining (e.g. Ni mining by *Alyssum*) but then again the labour costs would make it inefficient. In the future, maybe better methods can be developed.

Later, during studies in the tropics (see Sect. 6), some heavy metal tests were carried out. We wanted to know in what concentrations essential trace metals are present. As one example, the manganese (Mn) content in tree fern fronds in a montane rainforest in Costa Rica was studied (Weber and Breckle 1994). Volcanic soils are rich in Mn; at the end of the rainy season (December–January), the content is lower than during the dry season (February–March) or at the end of the dry season (end of March) (Fig. 18). Additionally, it is remarkable how the Mn content differs between species.

4 High Mountains and Altitudinal Stress

In the summer of 2002, an expedition to the Pamir area was organized. After 34 years, a view to Afghanistan across the Tajik–Afghan border at the Abe Panj, the upper tributary of the Amu Darya, was again possible (Fig. 19a). This expedition – in the footsteps of my close friend Okmir Agakhanjanz (who had died a few months earlier) – was the first German expedition since the 1935 German Pamir expedition,

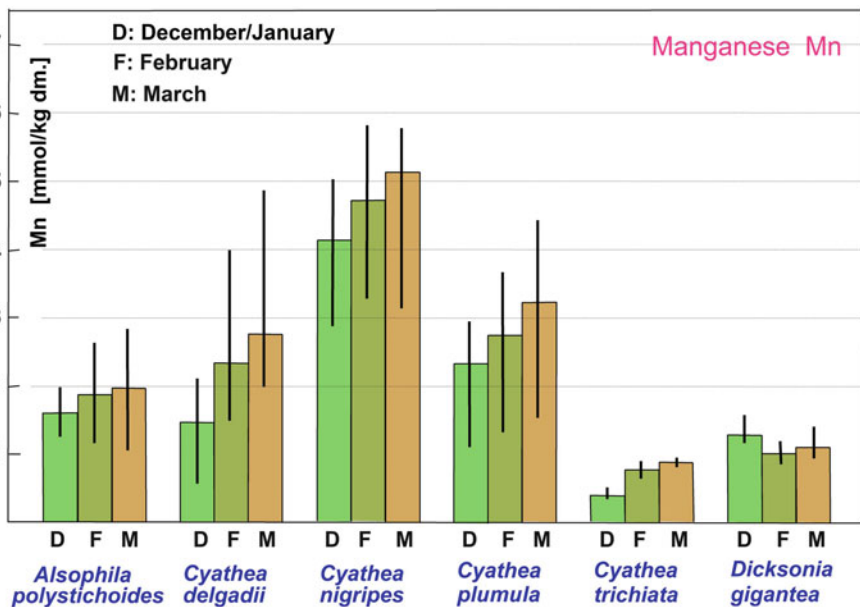


Fig. 18 Manganese (Mn) content ($\text{mmol kg}^{-1} \text{ dm}$) in six tree fern fronds in the montane tropical forest near Rio Lorenzito in the Sierra de Tilarán, Costa Rica, during the wet season (December) and dry season (March) (Weber 1994; Weber and Breckle 1994)

along the upper Abe Panj and Pamir River, and reaching Zorkul (at an altitude of 4,200 m), the lake being one of the sources of the Amu Darya. The contrasts between western and eastern Pamir in terms of landscape morphology, climate and vegetation were striking. Also the comparison of old vegetation maps (Vanselow et al. 2016) and the present-day situation showed strong desertification.

The expedition to the high mountain deserts of eastern Pamir enabled a survey and comparison of mountain ecological conditions between eastern and western Pamir. This was the last research trip of Clas Naumann, during which he finally clarified the biology of the moth *Zygaena pamira* (Fig. 19b, c); at 4,250 m the eggs were found developing on the lower side of yak cow dung, close to our campsite.

An almost symbolic plant of eastern Pamir is *teresken* (*Ceratoides papposa*, Fig. 19d). This species has an enormous geographical distribution (from the Ebro basin in Spain, the Vienna area and Pannonia to Mongolia and western China) in deserts and semi-deserts. *Teresken* has been the main energy source for the people since the break-up of the Soviet Union and the civil wars in Tajikistan, and is also the main fodder for sheep and goats, for donkeys and camels, and for the famous Marco Polo sheep (*Ovis ammon polii*). But, interestingly, *teresken* is a rather slow-growing dwarf shrub with a shoot-to-root ratio of up to 1:40, thus it is very drought resistant. For fuel, the woody root is used. Old plants have a thick rootstock and can reach 130 years of age (Walter and Breckle 1994).

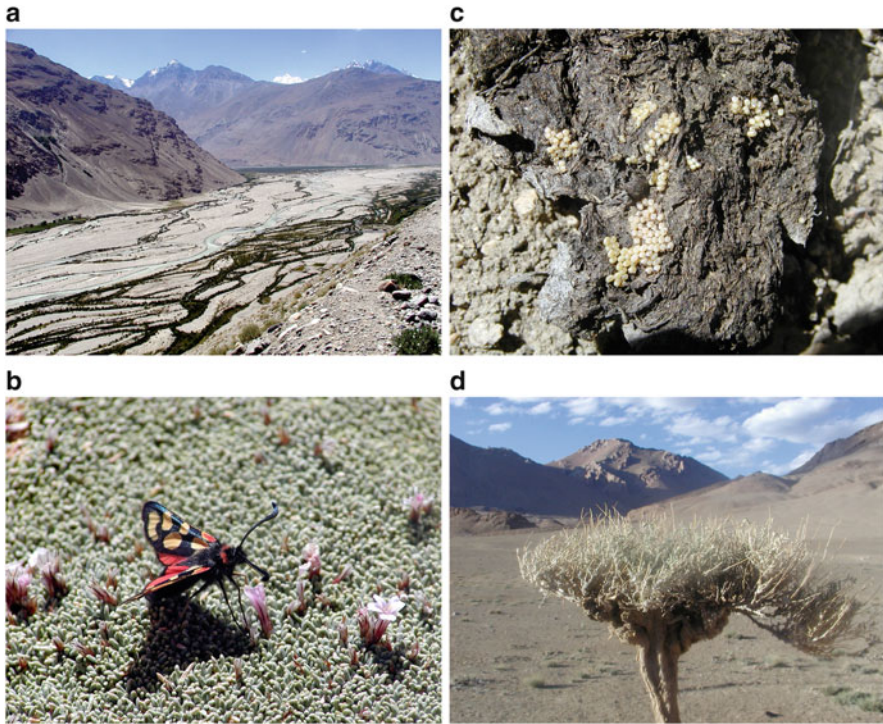


Fig. 19 (a) The Pamir River, Tajikistan, with meandering parts and natural gallery forests, joining the Wakhan River in the background (Afghanistan) (photo courtesy of C. Naumann, 2002). (b) *Zygaena pamira* on *Acantholimon diapensioides* at Turumtaikul (4,200 m), Pamir (photo courtesy of C. Naumann, 2002). (c) *Zygaena pamira* egg layings on the lower side of yak cow dung at Turumtaikul, Pamir (photo courtesy of C. Naumann, 2002). (d) *Krascheninnikovia ceratoides* (*teresken*), a middle-aged dwarf shrub, with thick woody rootstock, from eastern Pamir (photo: S. W. Breckle, 2002)

The “*teresken* syndrome” is one of the major problems in the eastern Pamir region and urgently needs a solution through replacement of *teresken* with other energy sources (projects from non-governmental organizations [NGOs] have started). A very similar and astonishingly parallel problem is the “*tola* syndrome” in the dry altiplano of Bolivia, where, again, people depend on almost only one life form. Again, slow-growing dwarf shrubs of the composite *Parastrephia* are the main source of fuel and fodder for lamas, alpacas and also the wild camelid vicuñas (Breckle and Wucherer 2006; Ahmadov et al. 2006).

Flora of high mountains is derived from floristic ancestors on the plains and in adjacent lower hill areas. In the Central Asian mountains, the migration of species, evolution of new species and extinction of species are leading to new mountain flora (Agakhanjanz and Breckle 1995). The character and speed of orogenesis, the climatic situation, the stages of forest belts and, finally, glaciation are the governing factors. A comparative survey of the phyto-diversity and known species numbers in

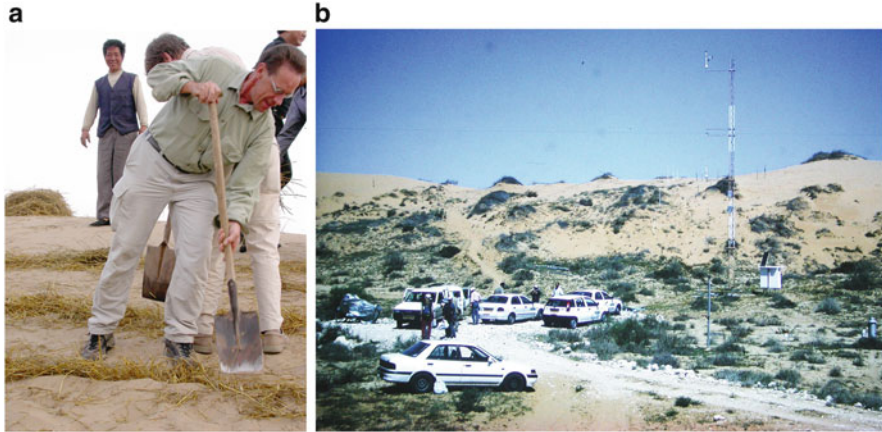


Fig. 20 (a) Combating desertification in Inner Mongolia. By a checker-straw technique, sand movement of mobile dunes is retarded, and diaspores of pioneer plants are able to invade within the straw squares (photo courtesy of C. Wissel, September 2004). (b) Nizzana sand dune area with longitudinal dunes (western Negev Desert); meeting of project groups (photo: S. W. Breckle, 1998)

the Eurasian mountains clearly indicates the need for small-scale inventories, especially for the orophytic belt (above the timberline). There endemics reach a high proportion in the subalpine and alpine belts but are almost absent in the subnival and nival belts, where some widespread boreal and even arctic species are present (Agachanjanz and Breckle 2002; Breckle 2004). In contrast, in arid mountains lacking a forest belt, endemics are more common in the lower belts. Concerning the Hindu Kush, the main Afghan mountain range, see Sect. 7.2.

5 Desert Ecology

Stress ecology is certainly very relevant in deserts. Heat stress and drought stress are the prominent ecological factors that organisms have to be adapted to or avoid. All of those questions of desert research have also been part of desertification studies. Only a few examples can be mentioned here. Desertification on a large scale has also been seen in several parts of China (Veste et al. 2006; Gao et al. 2007), with a severe dust situation in Beijing. Large-scale afforestation projects with millions of trees being planted in the loess area and sand-binding actions (Fig. 20a) are under way.

In 1999, a competent network of German scientific institutions was founded in Bielefeld (DesertNet) for exchange and planning of innovative joint projects. Close contacts with relevant political institutions were built up. Especially with the Secretary of the United Nations Convention to Combat Desertification (UNCCD) in Bonn, fruitful discussions took place, as well as participation at the Expo 2000 in Hanover. Participating in political discussions on the means necessary for combating