Plant Physiological Ecology - Introduction, Approaches and History

Introductory Overview and Context:

We will address four questions in this course:

1. WHAT IS THE FIELD OF PLANT PHYSIOLOGICAL ECOLOGY?
2. WHAT DOES IT SEEK TO EXPLAIN OR UNDERSTAND ABOUT PLANTS?
3. HOW WILL WE APPROACH LEARNING ABOUT PLANT PHYSIOLOGICAL PROCESSES IN AN ECOLOGICAL CONTEXT?
4. WHAT ARE THE HISTORICAL ROOTS OF THIS AREA OF PLANT BIOLOGY?

Issues to be addressed:

- The issue of how to frame our approach to studying plant function in an ecological context
- The issue of how pattern arises in nature and what role "function" plants in explaining the pattern
- The issue of scale
- The issue of adaptation

• Studying plant function in an ecological context: one framework

Plants as "balanced" systems:

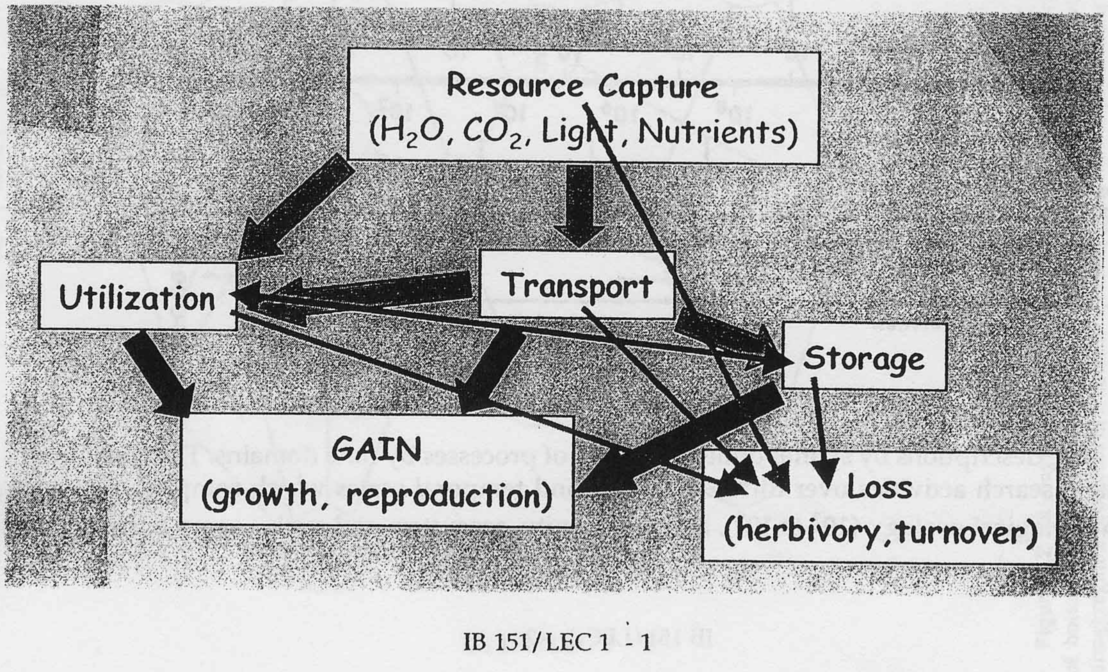
A. many complex, interacting processes exist in plants spanning spatial and temporal scales

B. plants can be viewed as "functional systems" where the systems is composed of traits that we might study. A single trait can be further viewed as an attribute possessed by a plant that aloow it to function well in a given environment. However, it is best to place single traits into the context of the whole plant as "system" of integrated functions operating in a relatively balanced manner. Atomizing traits into a laundry list of adaptations that compose the whole organism is dangerous - leads to adaptive storytelling. Telling a story about a trait should be a heuristic device, not a truth.

C. The outcome of "balanced" function is enhanced growth, survival, and reproductive success. As such, plant physiological ecology is about studying the BASIS of adaptation.

D. The kinds of factors to be considered in this course:

1. resources - water, CO_2, light, nutrients
2. resource state and distribution, where, what form, energy state
3. resource flow within plants



4. mechanisms for resource capture and utilization may be biochemical, physiological, or morphological and have differing time and spatial scales (Figures below).

• Pattern in nature and what role "functional biology" plays in explaining it

Patterns that we seek to explain:
→ patterns of form and function
→ patterns of vegetation change across landscapes

Perspectives on Pattern:
→ Ecologists seek to find the connections between patterns in the natural world and environmental conditions that are known to shape these patterns
→ Evolutionary Biologists seek to understand which environmental factors have shaped the 'adaptations' (form and function) that we see
→ Physiologists seek to discover the underlying mechanistic basis that have permitted some plants to live in a certain spot and not others

Within the context of studying pattern, plant physiological ecology tends to focus on:

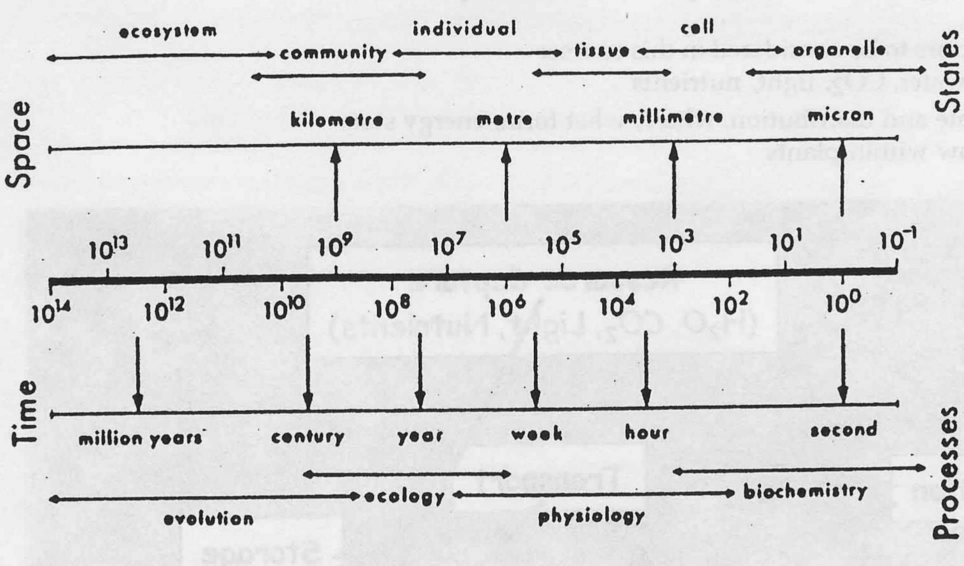
• **studies of how plants cope** (the study of performance at the interface between the organism and its biotic or abiotic environments = the basis of adaptations) – elaborated on below

• **studies that elucidate the role of plants in shaping community- and/or ecosystem-level patterns and process** (the study of how performance traits influence the ways in which energy and materials flow through a particular system) – related to the scaling issues and the interface with ecosystem ecology

• Scale and scaling

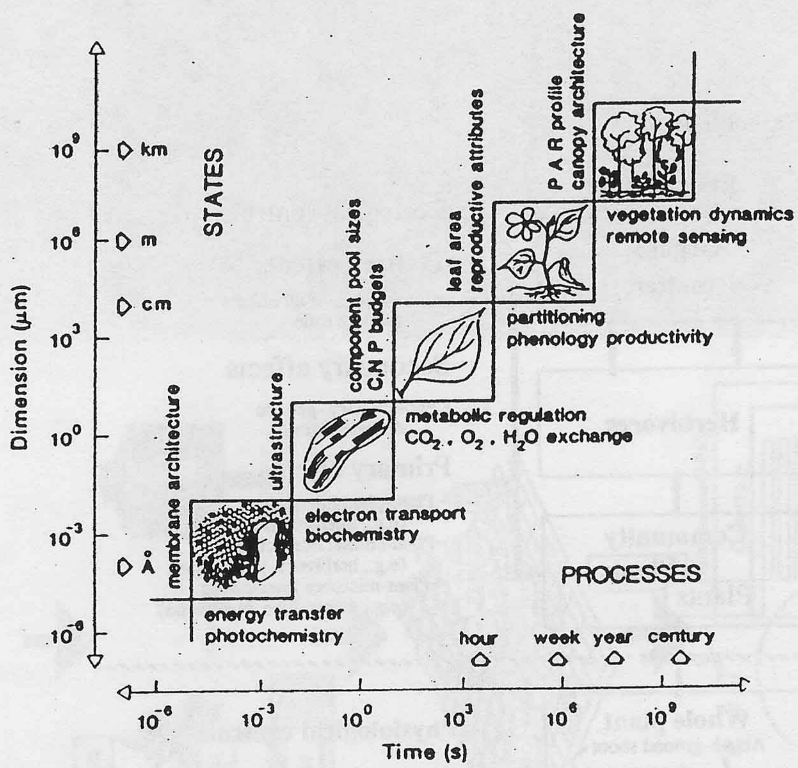
Physiological plant ecology today is a field that is attempting to bridge many scales of function and is being used to bridge fields (e.g., ecology and physiology, physiology and evolutionary biology).

The Space–Time Scale

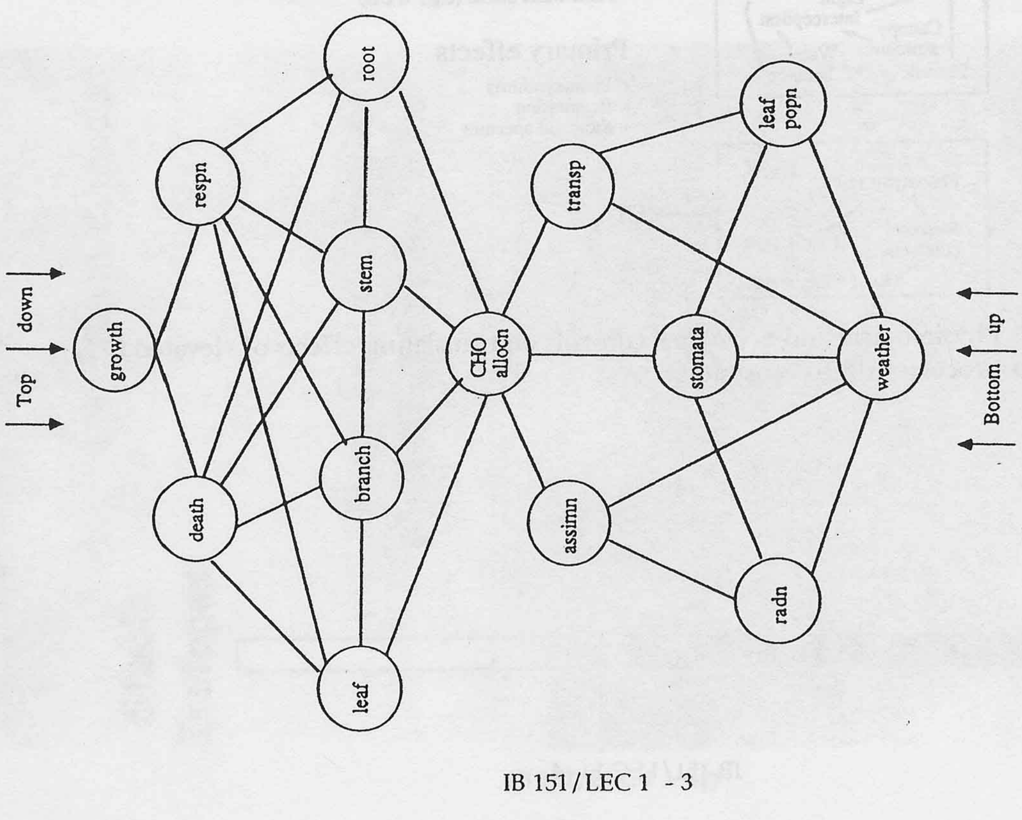


The "scaling" of state descriptions by spatial dimensions and of processes by time domains. The continuum demonstrates the research activities over different spatial and temporal scales which comprise physiology (10^{-1} to 10^{1}), physiological ecology (10^{1} to 10^{8}), and community, ecosystem and evolutionary ecology ($>10^{8}$).

Both **measurements** and **modeling** are being applied very effectively in scaling among different levels of organization, providing the backdrop for developing scaling "rules, and testing these rules and models



An arbitrary scaling of relevant states (defined by approximate "order-of-magnitude" [base 10] dimensions in micrometers) and processes (defined by approximate "order-of-magnitude" [base 10] time dimensions in seconds. From Osmond and Wong (1988; Australian Journal of Plant Physiology 15: 1-9).



Paul G. Jarvis

Figure 6.2 A diagram of a plant or stand growth model to illustrate the convergence of bottom-up and top-down approaches to the prediction of growth. Assembly of the disaggregated processes in a bottom-up model may lead to predictions of growth. In a top-down model, growth may be related to absorbed radiation (radn) by an empirical function, the lumped parameter(s) in that function being explained or derived by identifiable processes at successive levels of detail.

James F. Reynolds et al.

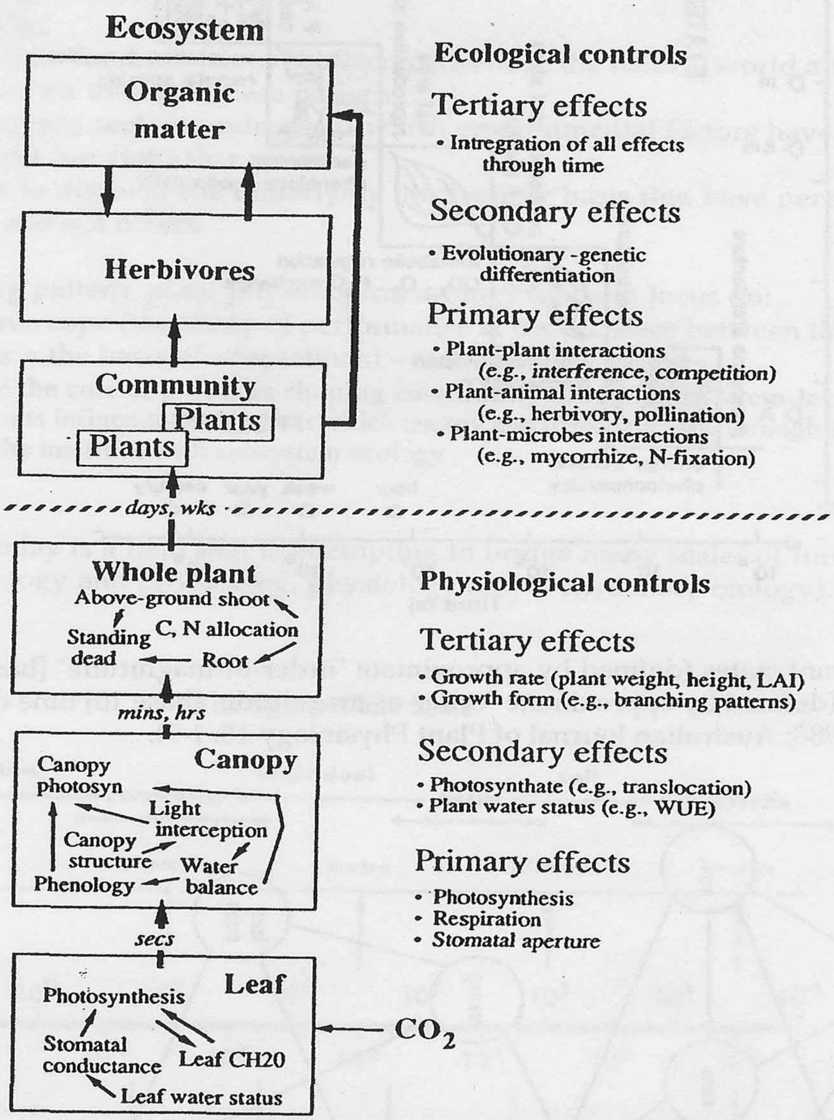
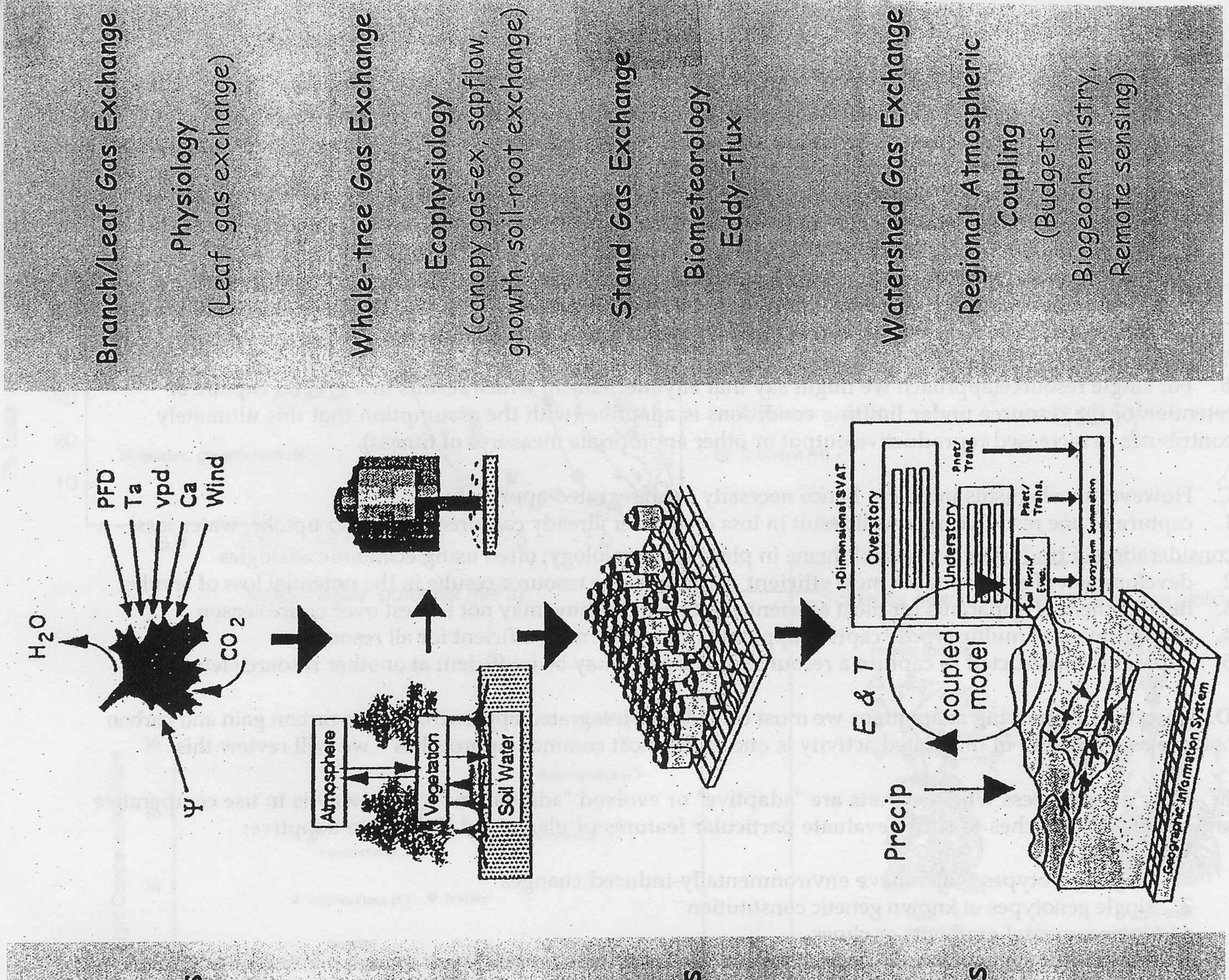


Figure 7.1 Physiological and ecological controls on translating effects of elevated CO_2 from leaf-level processes up to ecosystems.


Scaling Approach
Stable Isotopes
Plant-level Controls
Plant-level Controls & Plant-Environ Feedbacks
Environmental Controls
Climate Controls
H_2O
CO_2
PFD
Ta
Vpd
Ca
Wind
Ψ
Atmosphere
Vegetation
Soil Water
E & T
coupled model
Precip
1-Dimensional SVAT
Overstory
Understory
Geographic Information System
Branch/Leaf Gas Exchange
Physiology
(Leaf gas exchange)
Whole-tree Gas Exchange
Ecophysiology
(canopy gas-ex, sapflow, growth, soil-root exchange)
Stand Gas Exchange
Biometeorology
Eddy-flux
Watershed Gas Exchange
Regional Atmospheric Coupling
(Budgets, Biogeochemistry, Remote sensing)

• Adaptations

What is adaptive?

A. Philosophy - While it is easily accepted that organisms are adapted to the environments in which they naturally occur, it is often more difficult to assess whether we have identified an adaptation. Further, it is often very challenging to assign an adaptive value to a specific feature isolated from the rest of the biology of that organism or the evolutionary circumstances under which the adaptation arose. For organisms that are long-lived (not annual) and where recruitment of new individuals into the population occurs at irregular intervals, it can also be equally challenging to provide an unequivocal measure of that organism's fitness in terms of either specific adaptive features or differential reproductive contributions to the next generation. These constraints, however, should not be deterrents to the study of adaptive features in plants (see Ackerly et al. 2000).

B. For single resource approach we might say that any mechanism which results in a greater capture or retention of the resource under limiting conditions is adaptive (with the assumption that this ultimately contributes to increased reproductive output or other appropriate measures of fitness).

C. However mechanisms interact - hence necessity for integrated approach;

1. capture of one resource may well result in loss of another already captured (e.g., CO_2 uptake, water loss) - a consideration of tradeoffs is a central theme in plant ecophysiology; often using economic analogies
2. development of apparatus for most efficient capture of one resource results in the potential loss of another
3. development of apparatus for most efficient capture at one time may not be best over entire season
4. configuration of multipurpose capture apparatus cannot be most efficient for all resources
5. apparatus constructed to capture a resource at one level may be inefficient at another resource level

D. Therefore in studying adaptations we must consider an integrated approach. Use of carbon gain and carbon balance as a measure of integrated activity is one of the most common approaches – we will review this.

E. How do we assess whether traits are "adaptive" or evolved "adaptations"? ; one way is to use comparative and genetic approaches to study evaluate particular features of plants and if they are adaptive;

1. ecotypes
2. single genotypes which have environmentally-induced changes
3. single genotypes of known genetic constitution
4. environmental gradients or clines
5. convergent forms - commonality of plant response in holoclimates (even though plants may be of divergent phylogenetic background)

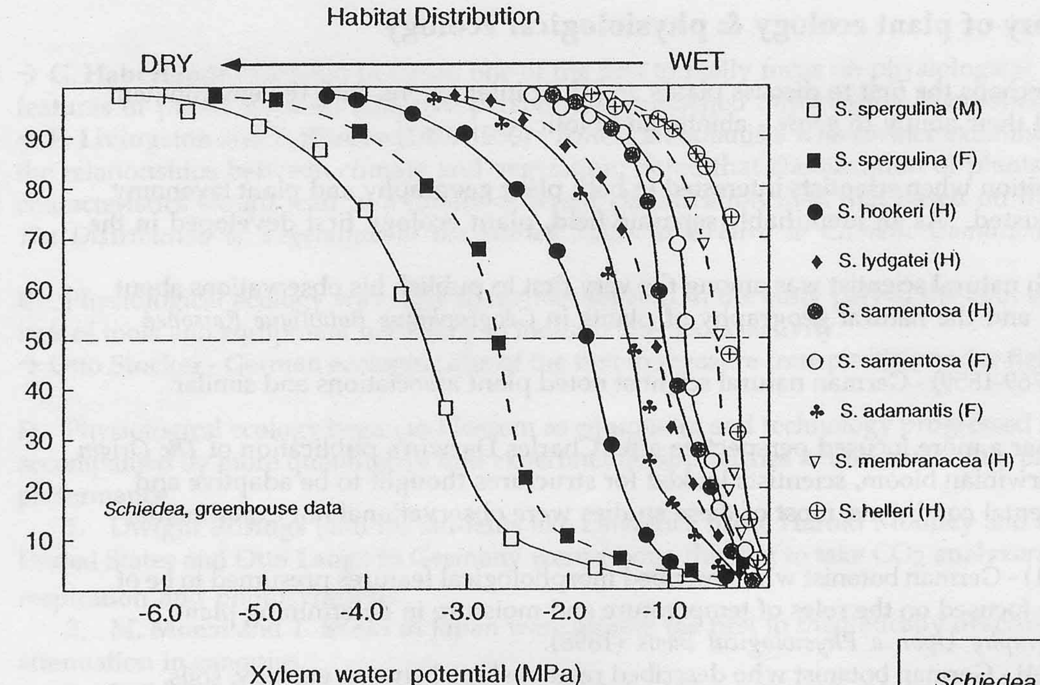
F. Some important terminology:

adaptation - feature(s) of an organism which allow it to persist in an environment

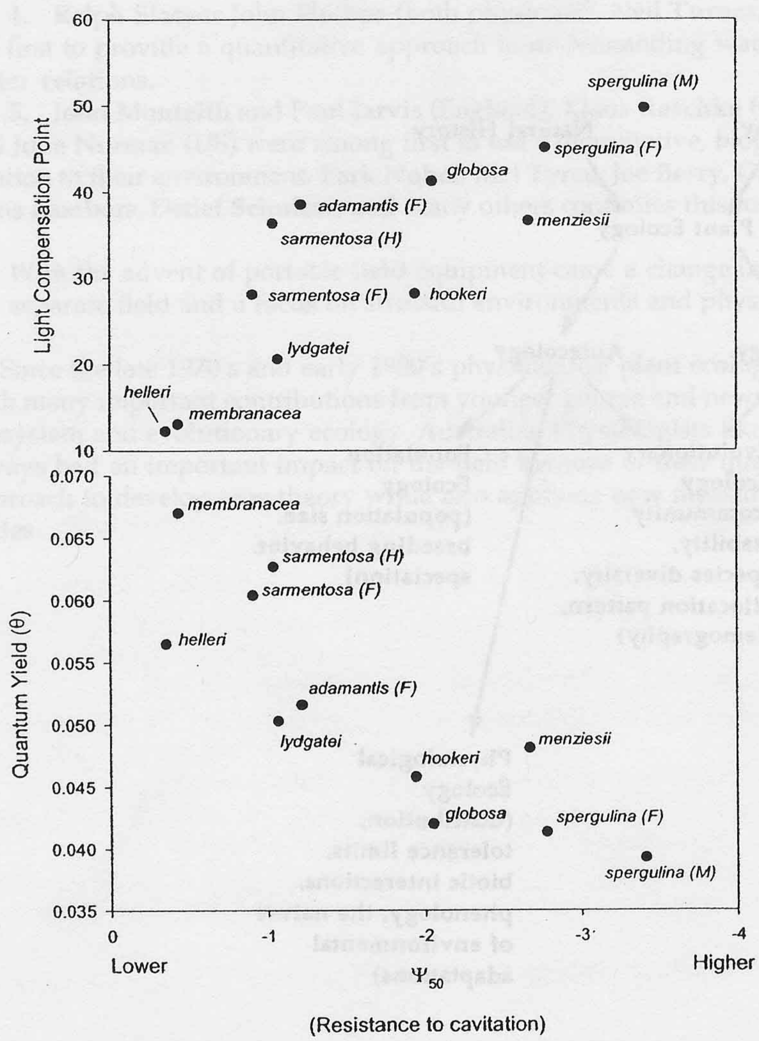
acclimation - ability of a genotype to express multiple phenotypes in response to an environmental fluctuation

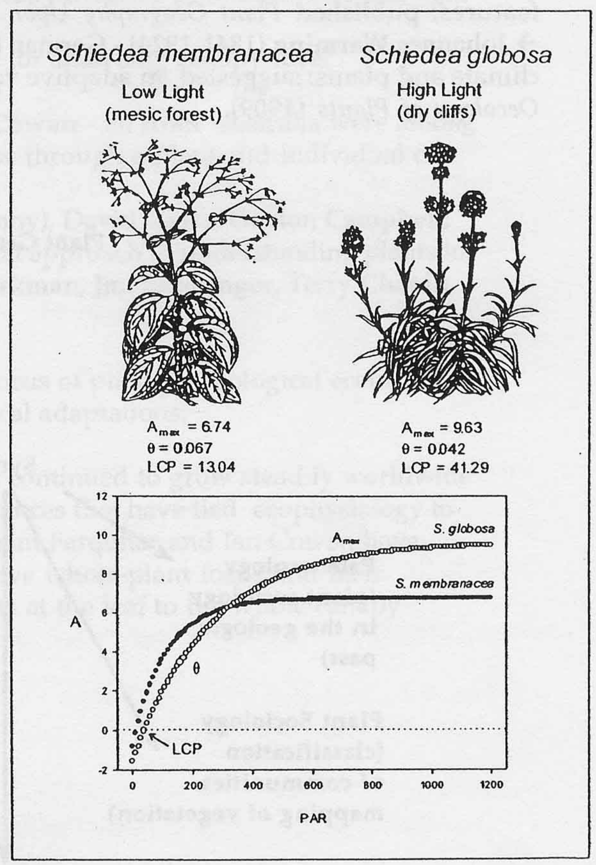
exaptation - feature of an organism which originally evolved for one function, but may now have [adaptive] value under a different set of circumstances

adaptive radiation - proliferation of a phylogenetic line into multiple environments (usually thought to occur when new environments open up or when there is a lack of competitors or when those particular niches are unfilled by other organisms)



Example of Adaptive Radiation in physiology (after Dawson et al. 2005)



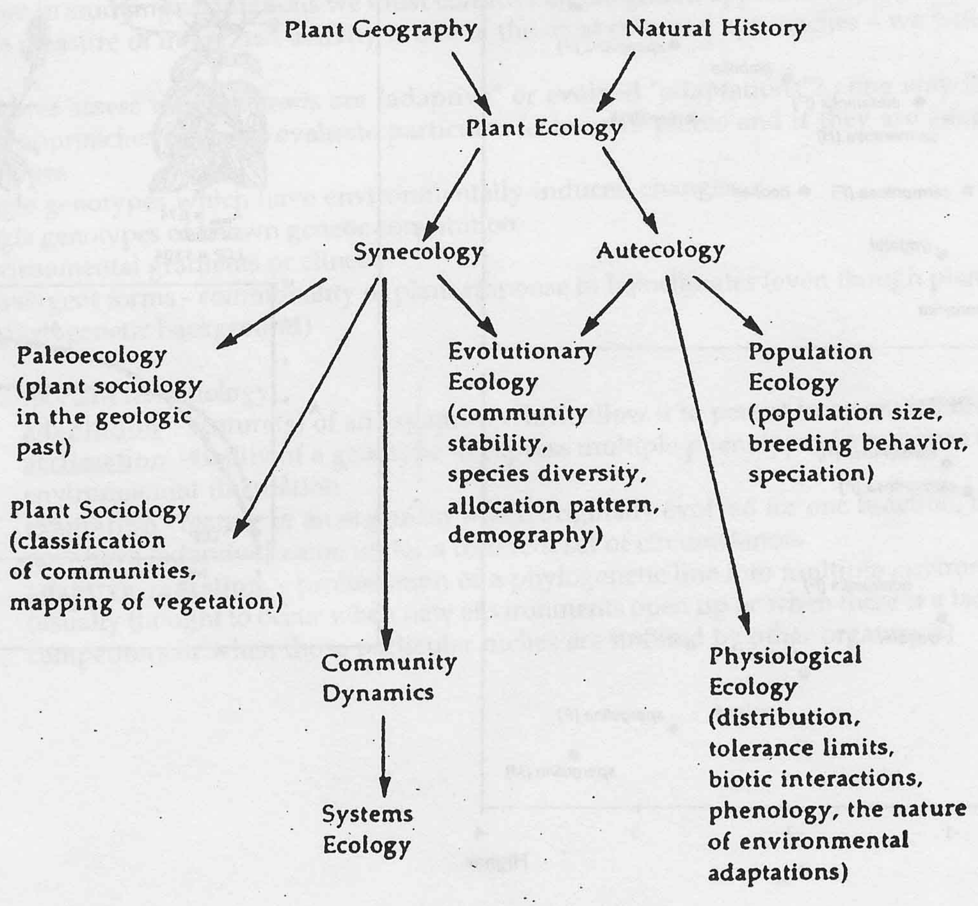


APPENDIX : A brief history of plant ecology & physiological ecology

A. **Theophrastus** (300 B.C.) - Perhaps the first to discuss plants and their interactions with the environment with firm ideas of what limited their ability to grow - abiotic and biotic.

B. Plant ecology gained recognition when scientists interested in both plant geography and plant taxonomy realized that a separate field existed. As an identifiable separate field, plant ecology first developed in the 19th century with:
→ André I. **de Candolle** - French natural scientist was among the very first to publish his observations about plant-environment interactions and the natural geography of plants in *Géographique Botanique Raisoneé* (1855)
→ Alexander **von Humboldt** (1769-1859) - German natural scientist noted plant associations and similar

C. Plant geography took another a more focused perspective after Charles Darwin's publication of *The Origin of Species* (1859). In the post-Darwinian bloom, scientists looked for structures thought to be adaptive and associated these with environmental conditions; most of these studies were observational not experimental (figure below).
→ Andreas **Schimper** (1856-1901) - German botanist who described morphological features presumed to be of adaptive value; in particular, he focused on the roles of temperature and moisture in determining plant features; published *Plant Geography Upon a Physiological Basis* (1898).
→ Johannes **Warming** (1841-1924) - German botanist who described relationships between geology, soils, climate and plants; suggested an adaptive value to morphological features and to life forms; published *Oecology of Plants* (1909).



→ G. **Haberlandt** - German botanist; one of the first to really focus on physiological, cellular, and biochemical features of plants from an adaptive perspective; published *Physiological Plant Anatomy* (1884).
→ B. **Livingston** and F. **Shreve** (1878-1950) - American botanists who further examined in a quantitative manner the relationships between climate and vegetation; noted that classification of plants according to leaf characteristics would lead to a totally different classification than that based on floral characters; published *The Distribution of Vegetation in the United States as Related to Climatic Conditions* (1921).

C. Physiological ecology was slow to further develop in the early part of the 20th century, largely due to the lack of tools and equipment necessary to measure metabolic activity.
→ Otto **Stocker** - German ecologist; one of the first to measure transpiration under field conditions.

D. Physiological ecology began to blossom as equipment and technology progressed in the 1950's. This was accompanied by more quantitative and experimental approaches to understanding plant function and performance.

1. Dwight **Billings** (and his students like Lawrence **Bliss**, Harold **Mooney** and Martyn **Caldwell**) in the United States and Otto **Lange** in Germany were among the first to take CO_2 analyzers into the field to measure respiration and photosynthesis.
2. M. **Monsi** and T. **Saeki** in Japan were among the first to theoretically describe photosynthesis and light attenuation in canopies.
3. F. **Eckhardt** in France was among the first to develop equipment for analyzing canopy-level photosynthesis in the field, making a whole-plant perspective possible.
4. Ralph **Slatyer** John Phillips (both physicists), Neil **Turner**, Ian **Cowan** - all from Australia were among the first to provide a quantitative approach to understanding water flow through a plant and individual cell water relations.
5. John **Monteith** and Paul **Jarvis** (England), Klaus **Raschke** (Germany), David **Gates**, Gaylon **Campbell**, and John **Norman** (US) were among first to use a quantitative, biophysical approach to understanding plants in relation to their environment. Park **Nobel**, Mel **Tyree**, Joe **Berry**, Ola **Bjorkman**, Jim **Ehleringer**, Terry **Chapin**, Hans **Lambers**, Detlef **Schultze**, and many others continues this today.

E. With the advent of portable field equipment came a change in the focus of plant physiological ecology as a separate field and a focus on stressful environments and physiological adaptations.

F. Since the late 1970's and early 1980's physiological plant ecology has continued to grow steadily worldwide with many important contributions from younger people and newer advances that have tied ecophysiology to ecosystem and evolutionary ecology. Australian Physiologists like Graham Farquhar and Ian Cowan have always had an important impact on the field because of their quantitative whole-plant focus and their approach to develop new theory while also applying new measurements at the leaf to the whole-canopy scales.

Some Literature providing a historical view of Physiological Ecology

Billings, W.D. 1980. American deserts and their mountains: an ecological frontier. Bull. Ecol. Soc. 61:203-209.

Billings, W.D. 1985. The historical development of physiological plant ecology, p. 1-15. In: B.F. Chabot and H.A. Mooney (eds.), *Physiological Ecology of North American Plant Communities*. Chapman and Hall, New York.

Clausen, J., D. D. Keck, and W. M. Hiesey. 1940. *Experimental Studies on the Nature of Species*. Carnegie Inst. Wash. Publ. 520.

Clements, F.E. 1907. *Plant Physiology and Ecology*. Holt, New York.

DeLucia, E.H., J.S. Coleman, T.E. Dawson and R.B. Jackson. 2001. Plant Physiological Ecology: Challenges and New Horizons. *New Phytologist* 149: 12-16.

Haberlandt, G. 1914. *Physiological Plant Anatomy*. MacMillan & Co., London. (English translation)

Livingston, B. E., and F. Shreve. 1921. *The Distribution of Vegetation in the United States as Related to Climatic Conditions*. Carnegie Inst. Wash. Publ. 284.

Maximov, N. A. 1929. *The Plant in Relation to Water*. George Allen and Univin Ltd., London.

McIntosh, R. P. 1985. *The Background of Ecology Concept and Theory*. Cambridge University Press, Cambridge. 383 pp.

Mooney, H. A., R. W. Pearcy, and J. Ehleringer. 1987. Plant physiological ecology today. BioScience 37:18-20.

Schimper, A. F. D. 1898. *Plant Geography Upon a Physiological Basis*. Clarendon Press, Oxford. (English edition)

Slatyer, R. O. 1967. *Plant-water Relationships*. Academic Press, New York. 366 pp.

Turesson, G. 1922. The genotypical response of the plant species to the habitat. Heriditas 3:211-350.

Warming, E. 1909. *Oecology of Plants: An Introduction to the Study of Plant Communities*. Oxford Univ. Press, Oxford. (English translation).

Some Plant Physiological Ecology Texts

Chabot, B.F., and H.A. Mooney (eds.), *Physiological Ecology of North American Plant Communities*. Chapman and Hall, New York.

Coombs, J., D.O. Hall, S.P. Long, and J.M.O. Scurlock (eds.). 1985. *Techniques in Bioproductivity and Photosynthesis*. 2nd Edition. Pergamon, Oxford.

Fitter, A.H., and R.K.M. Hay. 1981. *Environmental Physiology of Plants*. Academic Press, London.

Fritschen, L.J., and L.W. Gay. 1979. *Environmental Instrumentation*. Springer Verlag, Heidelberg.

Givnish, T.J. (ed.). 1986. *On the Economy of Plant Form and Function*. Cambridge University Press, Cambridge.

Jones, H.G. 1992. *Plants and Microclimate*. Cambridge University press, Cambridge.

Kozlowski, T.T., P.J. Kramer, and S.G. Pallardy. 1991. *The Physiological Ecology of Woody Plants.* Academic Press, Inc., New Tork.

Lambers, H., F.S. Chapin III, and T.J. Pons. 1998. *Plant Physiological Ecology.* Springer, New York.

Lange, O., L. Kappen, and E.-D. Schulze (eds.). 1976. *Water and Plant Life.* Ecological Studies 19. Springer-Verlag, Berlin, Heidelberg, New York.

Larcher, W. 1995 (3rd Ed.). *Physiological Plant Ecology.* Springer-Verlag, Berlin, Heidelberg, New York.

Marshall, B., and F.I. Woodward. 1985. *Instrumentation for Environmental Physiology.* Cambridge University Press, Cambridge.

Monteith, J. L. and Unsworth. 1990. *Principles of Environmental Physics.* Edward Arnold Ltd., London, Second Edition.

Nobel, P.S. 1991. *Physicochemical and Environmental Plant Physiology.* Academic Press, Inc., New York.

Osmond, C. B., O. Björkman, and D. J. Anderson. 1980. *Physiological Processes in Plant Ecology.* Ecological Studies 36. Springer-Verlag, Berlin, Heidelberg, New York.

Pearcy, R.W., J.R. Ehleringer, H.A. Mooney, and P.W. Rundel. 1989. *Plant Physiological Ecology Field Methods and Instrumentation.* Chapman and hall, New York.

Sestak, Z., J. Catsky, and P.G. Jarvis (eds.). 1971. *Plant Photosynthetic Production, Manual of Methods.* W. Junk, The hague.

Turner, N. C., and P. J. Kramer (eds.). 1980. *Adaptations of Plants to Water and High Temperature Stress.* Wiley-Interscience, New York.

Woodward, F.I. 1987. *Climate and Plant Distribution.* Cambridge University Press, Cambridge. 174 pp.

Other Articles and Books focused on Plant Physiological Ecology

Ackerly, D.D., S.A. Dudley, S.E. Sultan, J. Schmitt, J.S. Coleman, R. Linder, D.R. Sandquist, M.A. Geber, A.S. Evans, T.E. Dawson and M.J. Lechowicz, 2000. The evolution of plant ecophysiological traits: recent advances and future directions. *BioScience* 50(11): 979-995.

Bazzaz, F. A. 1979. The physiological ecology of plant succession. Annual Review Ecology Systematics 10:351-371.

Bazzaz, F.A., N.R. Chiariello, P.D. Coley, and L.F. Pitelka. 1987. Allocating resources to reproduction and defense. BioScience 37:58-67.

Boardman, N. K. 1977. Comparative photosynthesis of sun and shade plants. Annual Review Plant Physiology 28:355-377.

Campbell, G.S. 1977. An Introduction to Environmental Biophysics. Springer Verlag, New York. 159 pp.

Chapin, F.S. III., A.J. Bloom, C.B. Field, and R.H. Waring. 1987. Plant responses to multiple environmental factors. BioScience 37:49-57.

Crawly, M.J. (ed.). 1997. Plant Ecology. 2nd Edition. Blackwell Scientific Publications, Oxford.

Donald, C. M. 1961. Competition for light in crops and pastures. In: Mechanisms in Biological Competition. Symposium Society Experimental Biology 15:282-313.

Evans, J.R., S. von Caemmerer and W.W. Adams (eds.). 1988. Ecology of Photosynthesis in Sun and Shade. CRIRO Publications, Canberra, Australia.

Fisher, R. A., and N. C. Turner. 1978. Plant productivity in the arid and semiarid zones. Annual Review Plant Physiology 29:277-317.

Fitter, A.H., and R.K.M. Hay. 1981. Environmental Physiology of Plants. Academic Press, New York. 355 pp.

Gates, D. M. 1980. Biophysical Ecology. Springer-Verlag, New York.

Gates, D. M., and R. B. Schmerl. 1975. Perspectives in Biophysical Ecology. Ecological Studies No. 12. Springer-Verlag, New York.

Givnish, T.J. (ed.). 1986. On the Economy of Plant Form and Function. Cambridge University Press, Cambridge. 717 pp.

Grace, J. 1977. Plant response to Wind. Academic Press, New York. 204 pp.

Grime, J.P. 1979. Plant Strategies and Vegetation Processes. John Wiley and Sons, New York. 222 pp.

Harper, J. L. 1967. A Darwinian approach to plant ecology. Journal Ecology 55:247-270.

Harper, J.L. 1977. Population Biology of Plants. Academic Press, New York. 892 pp.

Hatch, M. D., C. B. Osmond, and R. O. Slatyer (Eds.). 1971. Photosynthesis and Photorespiration. Wiley Interscience, New York.

Jones, H.G. 1983. Plants and Microclimate. Cambridge University Press, Cambridge. 323 pp.

Landsberg, J.J. 1986. Physiological Ecology of Forest Production. Academic Press, New York. 198 pp.

Lange, O., L. Kappen, and E. D. Schulze (Eds.). 1976. Water and Plant Life. Ecological Studies 19. Springer-Verlag, New York.

Lange, O.L., P.S. Nobel, C.B. Osmond, and H. Ziegler (eds.). 1982. Plant Physiological Ecology. vol. 12A-D. Encyclopaedia of Plant Physiology New Series. Springer Verlag, Heidelberg.

Larcher, W. 1995. Physiological Plant Ecology. 3rd Edition. Springer-Verlag, New York.

Lewis, M. C. 1972. The physiological significance of variation in leaf structure. Science Progress 60:25-51.

Monsi, M. 1968. Mathematical models of plant communities. In: F. Eckhart (Ed.), Functioning of Terrestrial Ecosystems at the Primary Production Level. UNESCO, Paris.

Monteith, J.L. & M.H. Unsworth. 1990. Principles of Environmental Physics. 2nd Edition. Edward Arnold Ltd., London. 291 pp.

Mooney, H. A., and M. West. 1964. Photosynthetic acclimation of plants of diverse origin. American Journal Botany 51:825-827.

Mooney, H. A. 1972. The carbon balance of plants. Annual Review of Ecology and Systematics 3:315-346.

Mooney, H. A. 1974. Plant forms in relation to environment, pp. 113-122. In: B. R. Strain and W. D. Billings (Eds.), Handbook of Vegetation Science. Part 6: Vegetation and Environment. Dr. Junk Publishers, The Hague.

Mooney, H. A. 1976. Some contributions of physiological ecology to plant population biology. Systematic Botany 1:269-283.

Mooney, H.A., and B. Chabot (eds.). 1985. Physiological Ecology of North American Plant Communities. Chapman and Hall, New York. 351 pp.

Mooney, H.A., W.W. Winner, and E.J. Pell. 1991. Response of Plants to Multiple Stresses. Academic Press, Inc., New York.

Nobel, P.S. 1983. Biophysical Plant Physiology and Ecology. W.H. Freeman and Company, New York. 608 pp.

Osmond, C.B., M.P. Austin, J.A. Berry, W.D. Billings, J.S. Boyer, J.W.H. Dacey, P.S. Nobel, S.D. Smith, and W.E. Winner. 1987. Stress physiology and the distribution of plants. BioScience 37:38-48.

Pearcy, R.W., O. Björkman, M.M. Caldwell, J.E. Keeley, R.K. Monson, and B.R. Strain. 1987. Carbon gain by plants in natural environments. BioScience 37:21-29.

Penning De Vries, F. W. T., A. H. M. Brunsting, and W. H. Van Laar. 1974. Products, requirements and efficiency of biosynthesis: a quantitative approach. Journal Theoretical Biology 45:339-377.

Rundel, P.W., J.R. Ehleringer and K.A. Nagy. Stable Isotopes in Ecological Research. Ecologigal Studies 68, Springer-Verlag.

Schulze, E.-D., R.H. Robichaux, J. Grace, P.W. Rundel, and J.R. Ehleringer. 1987. Plant water balance. BioScience 37:30-37.

Silvertown, J. 1987. An Introduction to Plant Population Ecology. Second Edition. John Wiley and Sons, New York. 229 pp.

Smith, H. (ed.). 1981. Plants and the Daylight Spectrum. Academic Press, New York. 508 pp.

Solbrig, O. T., S. Jain, G. B. Johnson, and P. H. Raven (Eds.). 1979. Topics in Plant Population Biology. Columbia University Press, New York.

Vogel, S. 1981. Life in Moving Fluids - The Physical Biology of Flow. Princeton University Press, Princeton. 352 pp.

Walter, H. 1985. Ecological Systems of the Geobiosphere. 1. Ecological Principles in Global Perspective. Springer verlag, Heidelberg. 242 pp.

Walter, H. 1986. Ecological Systems of the Geobiosphere. 2. Tropical and Subtropical Zonobiomes. Springer Verlag, Heidelberg. 465 pp.

Willson, M.F. 1983. Plant Reproductive Ecology. John Wiley and Sons, New York. 282 pp.

Woodward, F.I. 1987. Climate and Plant Distribution. Cambridge University Press, Cambridge. 174 pp.