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Environmental Physiology of Plants

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Environmental Physiology of Plants

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Preface

This book arose from the perception of a need for a text which examines the physiology of plants from an ecological and evolutionary standpoint. It is a curious observation that zoologists refer to the "grey area" between physiology and ecology as "environmental physiology", whereas botanists generally use the term "physiological ecology". The reason for this difference lies, perhaps, in the differing developments that physiology and ecology have undergone at the hands of plant and animal biologists. For zoologists ecology has always involved the study of populations, but botanists have only recently become aware of their importance. Plant ecology has been based, from its beginnings, on a distinction between synecology (the study of communities rather than populations) and autecology (the study of individual plants or plant species); the animal equivalent of autecology, in contrast, has tended to verge on behavioural studies, especially in the study of vertebrates. As a result the relationship of the individual organism to its environment was an early fascination of plant ecologists, and this, in turn, has led to the stress laid on "physiological ecology". The zoologist, however, came to the same problems from a primary interest in the physiology of organisms. It therefore comes as a surprise to find that the word ecology, at least in its modern sense, was coined by Haeckel, a zoologist, in 1886 as the "relation of the animal to its organic and inorganic environment".

This book is an attempt to bridge the gap between the physiology and biochemistry of plants on the one hand, and their ecological behaviour on the other, starting from this "zoological" standpoint. It asks the question: "how do the intricate physiological mechanisms which have been elucidated over the last 100 years by plant physiologists really operate under natural conditions?" The structure of the book is dictated by the underlying concept that plants sense the environment in two distinct ways: first, as a source of energy and materials, and second as a compendium of potentially damaging stresses. Thus Chapters 2 to 4 treat the environment as a fund of resources (light, minerals, water), whereas Chapters 5 to 8 examine the various environmental stress factors (temperature, toxins, and other organisms). The introductory Chapter serves to set the ecological and evolutionary framework within which plants operate. An important paradox in plant ecology is that, although there is an overall similarity amongst plant species in their biochemistry and physiology, evolution has acted on this uniformity to give ecological diversity. Consequently, within the factorial structure of this book, we have emphasized the importance of a comparative approach, recognizing the significance of inter-specific differences.

We have written this book for the use of second and third year undergraduates, as well as postgraduates, and have therefore been generous with literature references to encourage familiarity with original material. To those to whom "plants" means the whole plant kingdom we must apologize for the emphasis on Angiosperms: space and personal acquaintance are our excuses.

Finally we should thank all those colleagues who have read parts of the manuscript: their comments were invaluable. They were as follows: Chapter 1 (A.H.F.)—A. D. Bradshaw, T. J. Crawford; Chapter 2 (A.H.F.)—J. P. Grime; Chapter 3 (A.H.F.)—P. B. Tinker; Chapter 4 (R.K.M.H.)—W. J. Davies, T. A. Mansfield, E. I. Newman; Chapter 5 (R.K.M.H.)—J. A. Bryant; Chapter 6 (A.H.F.)—M. J. Chadwick; Chapter 7 (R.K.M.H.)—J. A. Bryant, T. A. Mansfield; Chapter 8 (A.H.F.)—J. H. Lawton, M. H. Williamson. In addition Professor J. F. Sutcliffe read the entire manuscript and made valuable comments.

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January, 1981

A. H. Fitter
R. K. M. Hay

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Part I

Introduction

1. The Physiological Basis of Ecology

The canals of Mars and a wealth of twopenny science fiction testify to the pedigree of Man's belief that life could exist on other planets. But when Jules Verne took his improbable train to the moon his expectation of encountering living creatures was not based on knowledge of the versatility of living systems, but on ignorance of the real conditions on other planets. We know enough of those environments to persuade any rational Victorian that they must be as barren as the summit of Everest; yet in 1975 a vehicle was launched to Mars to look for evidence of life, with curiously ambiguous, but probably negative results.

This strange paradox illustrates our new awareness of the ability of living systems on our own planet to withstand stress. Bacteria are now known which can persist at temperatures as high as 90°C (Brock and Darland, 1970), and other simple organisms will tolerate equally bizarre stresses. The adaptive power of higher plants, with which this book is concerned, is less dramatic, but it is sobering to consider how few terrestrial environments admit no plant growth, and how plants have colonized man-made terrain well beyond their normally experienced environmental range, such as metal-mine spoil heaps.

The concept of "normal" and "extreme" ranges of an environmental factor highlights the great variability of all such factors, in both space and time. The few exceptions to this are consequently of little physiological or ecological significance. Nevertheless, most physiological experiments are performed in constant or optimal environments, for the excellent reason that only there can the basic physiological processes be studied. Outside the laboratory these same processes cope with great variation, for plants have colonized all but the most extreme environments. Volcanoes achieve temperatures too high and ice-caps too low for plants; a few deserts are too dry, and deep caverns are too dark. Only the oceans represent an apparently favourable environment uncolonized by higher plants, but the problems are not physiological, for they can tolerate salt water in salt marshes. It seems probable that the shore is too rough and the algal holdfast better than the roots of higher plants at maintaining a hold there, while unicellularity is the optimum form for the open sea.

Only a few species are capable of colonizing extreme environments, whereas more moderate environments can support many more. The diversity of species in a habitat is thus controlled by the environment, whether by soil fertility (Thurston, 1968), altitude (Del Moral, 1972a), or any other factor. This diversity reflects the number of species adapted to grow in the habitat, and the nature of this adaptation must be examined in the light of the physiological effect of the environmental factors making up the habitat, and of their variation in time and in space.

A. Favourability and Toxicity

It is valuable when considering the physiological impact of an environmental factor to distinguish between unfavourability and toxicity. In ecological terms, favourability is a concept of limited value, as its definition tends to circularity (Terborgh, 1973), but the ecological tautology hides a physiological point of substance: favourable conditions are those which permit maximum growth for most species. Certainly some plants will continue to respond in culture to high nitrogen levels, which are no longer useful or even deleterious to others (Bradshaw *et al.*, 1964; Fig. 1.1), but many of the species apparently adapted to the least "favourable" habitats, such as *Deschampsia flexuosa* (Hackett, 1965), will in fact grow far better in a monoculture in "favour-

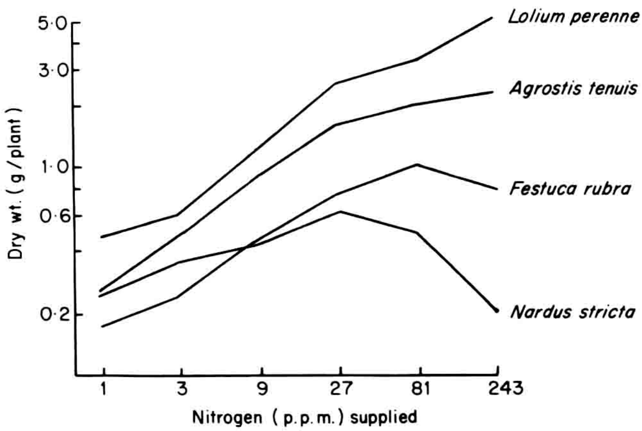

FIG 1.1. Effect of nitrogen supply on the dry weight of four grass species grown in sand culture for eight weeks. (From Bradshaw *et al.*, 1964).

able" conditions, and owe their ecological preference to low competitive ability and high tolerance of extremes.

There are then recognizable ranges of intensity for any environmental factor where most species fare best physiologically. Outside this range growth declines, but may do so for two distinct reasons. There may be an actual toxic effect, caused by excess of the factor, which actively interferes with metabolism. Excess lead ion, for example, inactivates many enzyme systems; excess salt may alter enzyme activity both directly and by reducing water potentials; and very low or high temperatures can bring about both structural damage and enzyme destruction. Such effects are manifestations of toxicity. On the other hand, in many cases there is no physical or chemical damage caused by the extreme conditions; simply a slowing down of metabolism occurs, through deficiency of nutrient ions, light or water. Since no damage is caused and full and typically immediate recovery is possible, these effects are best thought of as unfavourable.

For any factor, then, four states are possible: unfavourable, favourable, neutral, and toxic. At a given intensity the effect will vary with species and from the interaction of other factors. Thus optimum light intensity for photosynthesis depends on carbon-dioxide concentration (Fig. 1.2), and response to phosphate varies with nitrogen supply (Blair

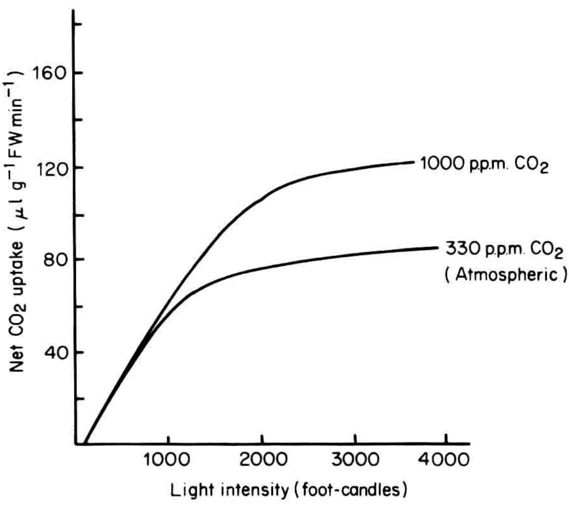

FIG. 1.2. Influence of CO_2 concentration on light-saturation of photosynthesis in bean leaves. At low light intensities CO_2 is not limiting and is without effect. (From Bidwell, R. G. S. (1979). "Plant Physiology". MacMillan, London).