A Functional
Biology of Crop Plants

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PREFACE AND ACKNOWLEDGEMENTS

This book is as much a broad and partially detailed research plan as it is a text. As a text it synthesizes the functional biological approach to higher plants from the initiatives of many researchers and my own research. It is not definitive even by default, because functional biology is not a mature field with fundamental principles agreed upon by all its practitioners; I hope to contribute to a needed unification. In some active fields of research such as salinity tolerance, I have stepped into strongly contested territory. I offer my attempts at resolution and synthesis as a contribution to the dialogue between holders of disparate views. Moreover, I hope that new research and under-standing will be generated from the synthesis and its new hypotheses. I also offer here an *apologia* for the functional biological approach (Sec. 1.C.ii), showing that it is not teleological. Rather, it generates with scientific rigor many fruitful and testable hypotheses of wide import that are not readily developed by approaches lacking a systems orientation. While one can use-fully "think like a plant" in order to generate hypotheses, functional biology does not ascribe purposiveness to organisms nor to evolution. Indeed, func-tional biology is singularly adapted to evaluating evolutionary dynamics.

As a text, this book is intended for advanced undergraduate and postgra-duate students with a background in plant physiology and a quantitative orientation. Calculus would be very helpful, though not critical to appreciat-ing the arguments developed herein. Conversely, I hope the book may be of interest to researchers in highly quantitative and systems-oriented disciplines who wish to expand their interests into a very promising field of biology. As a research plan, this book is intended for basic and applied researchers in physiology, ecology, and agronomy and for plant breeders and biotechnolo-gists, any of whom, it is hoped, will find major sections of interest. While I draw upon many evolutionary and ecological arguments about wild plants, the ultimate concern of this book is with crops, as the title states. Functional biology offers exciting prospects for the custom design of crop physiology, for timely implementation by the current breeders' art and by genetic engineering. With its new, quantitative, systems-oriented concepts, functional biology of crop plants should excite basic researchers. Since crop design is aimed directly at socially useful results, it should also interest the many peo-ple and institutions who apply and also fund research. In addition to the prospect of developing new routes to crop improvement, functional biology can also assess routes currently under intensive development in other discip-lines. Thus, it may help ensure that hard-won new initiatives such as transfer of nitrogen-fixation genes into plants will actually provide a net benefit, and the largest benefit. I invite direct inquiries from researchers and institutions,

concerning any topic developed in this book.

Numerous literature references are cited but the set is far from comprehensive on any given topic; rather, the references are meant to be illustrative. I regret that I had to forgo some topics of considerable interest and potential value, such as the effects of increased atmospheric carbon dioxide content and the evolutionary design of integrative control by plant hormones or growth substances.

For the very opportunity to write this book I am grateful to Croom Helm and the series editor for functional biology, Dr. Peter Calow. For the time and resources, I am indebted to my home institutions, the Department of Biology and the Plant Genetic Engineering Laboratory, and to my fine colleagues therein. Part of this book was written during my earlier tenure at the Los Alamos National Laboratory; I am grateful to my group leaders there, James Steger, Caroline Reynolds, and Eugene Wewerka. I wish to thank the numerous people who read the chapters and sections for content, style, and typography; I am responsible for any remaining errors. I thank especially Dr. Lou Ellen Kay, who read the manuscript in its entirety several times and directed me to new topics. Critiques of major sections were generously given by Drs. Rana Munns, John Passioura, R. A. Fischer, Emanuel Epstein, Thomas Sinclair, Richard Spellenberg, Fairley Barnes, Ralph Turner, James Pushnik, John S. Boyer, and Melvin Oliver.

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A. Functional Biology

Functional biology applied to plants explores how they capture and use resources and thus produce usable yield (crops) or ensure the long-term survival of the species and the genes (wild plants). Functional biology examines these results to ask *why* plants perform as they do, attempting to explain evolved function and to indicate how crops may be improved. The goal of most plant research, either proximately or ultimately, is generally the latter, finding out if and how we may improve crop performance. Functional biology enables us to develop quantitative, testable hypotheses about the optimality of plants' resource use. Potentially it allows us to determine the upper limits to crop performance. Some limits are known to fairly high specificity, as for leaf photosynthesis (Bassham, 1977; Gutschick, 1986). However, we still have little idea of other limits, such as the theoretical maximum yields for given degrees of salinity in the soil water. Functional biology can also suggest previously unsuspected routes to crop improvement, *e.g.,* breeding for specific leaf mass to optimize canopy photosynthesis (Chap. 3). A particular strength of functional biology is its potential to unify crop improvement efforts of diverse disciplines. Ultimately it promises to determine the single suite of physiological and morphological characteristics of a species that will give the greatest yield or other value indicator for a given environment (Sec. 1.D.i, item 2).

The mathematical expression of functional biology begins with proposing an objective function, which is the ultimate goal or value in the growth of the plant one is examining. For crops, this is typically yield, especially reproductive yield, or a related function (Secs. 1.B, 1.D.i). For wild plants, the objective function is typically a fitness measure such as the summed reproductive value of potential offspring. This goal is related tenuously to yield. In many aspects, agricultural goals may diverge very sharply from goals of wild growth, but plants continue to embody genetically some contrary wild-growth goals. Functional biology gives us a comprehensive framework to discern these conflicts and search for cost-effective remedies.

Once the objective function is proposed, one hypothesizes internal allocations such as root:shoot mass ratios or enzyme activity per leaf area that can be adjusted to maximize the objective function. The best internal allocation enables the plant to capture and use best all the external resources – minerals, water, CO_2, light. These resources generally pose the difficulties of

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being (1) quite dilute, hence energy-costly to acquire, (2) limited in total amount available, (3) imbalanced relative to one another, or (4) risky to acquire (more on risk soon). Acquisition and use of two different resources often conflict: growing more roots to acquire a dilute mineral element penalizes investment in shoot growth and therefore penalizes light capture. Similarly, performing photosynthesis to gain carbon uses soil water copiously and may exhaust it prematurely. Non-resources such as toxic heavy metals in the soil may also threaten plant functions.

The mode of analysis that many researchers find useful is to propose that plants deploy broad system strategies to achieve their goals. For example, a frequently postulated strategy is that plants minimize their use of metabolic energy in acquiring and using a resource such as soil nitrogen. Strategies act at a high level compounded from many elementary biochemical and morphological responses that are more commonly studied in isolation from each other. Strategies therefore integrate plant responses into a systems view, where it is possible to be quite inclusive and to ask what is the value to a plant of a definite, quantitative pattern of responses in elementary functions.

The identification of particular strategies may be inspired by observing more qualitatively the responses of plants to categories of environments. Grime (1979) analyzes plants as employing admixtures of three basic strategic complexes, which respectively classify plants as (1) competitors, (2) ruderals, having a sort of 'hit and run' pattern of resource use, and (3) stress-tolerators. Such analysis can be fruitful but it is in large measure an *a posteriori* or after-the-fact explanation of adaptive behavior. Townsend and Calow (1981) warn against such explanations as prone to being Panglossian, claiming that everything is done best in this, the best of worlds (Gould and Lewontin, 1979). Grime himself (1985) argues against naive adaptationist arguments. Nonetheless, while his three-strategies approach gives some qualitative guidance in developing testable hypotheses, it does not have an inclusive and quantitative set of principles for such purposes. Functional biology promises to provide these principles, on an *a priori* basis, to guard against adaptationism and to widen the scope of research while focusing more accurately. Functional biology also (and perhaps uniquely) offers the prospect of evaluating how nearly optimal various adaptations are in both kind and degree. These evaluations have value both in crop improvement research and in quantitative evolutionary studies.

Functional biology generally studies phenotypic adaptations – in the body wherein function is actually expressed – rather than genotypic adaptations that code for the phenotypic adaptations and that are the more penultimate objects of natural selection (genes persist, while individual bodies die). Townsend and Calow (1981) discuss the strengths and limitations of the narrowed viewpoint. We shall see that there is a great richness of insights within the phenotypic viewpoint.

B. The Requirements on Plants in Their Growth and Function

Wild plants simply must survive as species. As Slobodkin and Rapoport (1974) point out, one may view plants as participants in the evolutionary game of survival, provided that one views any 'winnings' such as increases in biomass or in number and vigor of offspring as being applicable only to continuing the game. Surviving does not generally mean attaining maximal yield or even reproductive mass, as we shall examine later. Competitive edges are not directly related to these two measures, which exclude consideration of the management of risk. Risks to long-term survival arise especially from environmentally-driven population fluctuations that can compound year-to-year to give rare extreme depressions of the population. The hope, not yet realized, is that we can quantify survival probabilities in wild plant growth from our knowledge of the biotic and abiotic challenges that plants experience, and that in consequence we can assign ultimate quantitative values to the adaptation of individual plants and explain the evolution of a species as a whole.

In agriculture, in contrast to wild growth, goals are enforced by humans.

(1) Historically, maximal yield was sought, using not only plant internal modifications but also extensive improvement of the environment by fertilization, irrigation, disease control measures, etc. More recently, an economically more tenable goal has come to the fore, at least implicitly–the goal of maximal monetary value of yield debited for the costs of the environmental improvements. The best compromise between yield and environmental improvement occurs when the incremental or marginal gain vanishes. Risk management has also become involved in agricultural goals, in an incompletely quantified form. Farmers may decline to grow cultivars giving the very best long-term average yield, if this yield is sufficiently unstable year-to-year that it unduly increases the prospect of a run of poor years that cannot be survived financially (Barry, 1984). Risk management considerations tend to narrow the divergence of wild-growth and agricultural goals.

Other points of difference between wild-growth and agricultural goals include:

(2) Wild forebears of crops optimize non-cooperative, competitive growth, while farmers desire the best concurrent or cooperative growth of all individual plants. Self-thinning (Harper, 1977) and the occurrence of plants of widely diverging heights and maturation dates are undesirable. Optimal sharing of resources is desired. Thus, crops have been bred with more erect leaves in order to share sunlight in the leaf canopy for greatest total growth; this feature did not and could not evolve in competitive wild growth. Agriculturalists have also, over thousands of years, bred out allelopathic responses of plants (Sec. 1.J) that retard the growth of competitors, even of congeners,

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because total yield can be improved. Lastly, in the wild the various individuals and species must deploy what are called "evolutionarily stable strategies" (Maynard Smith and Price, 1973), that is, strategies that are insusceptible to the invasion of 'cheaters' or non-cooperators. Some susceptibilities are immediately apparent. For example, a plant may restrict its use of soil water in order to optimize the schedule of use of this water. However, a competing plant may readily claim this resource as its own. In general, the possibility of invasion or conflict requires adjustments in the autecological strategies of all competitors, even to the detriment of their combined growth as measured by total biomass. One may say that evolutionary stability is assessed globally in time, rather than locally in today's environment. In evaluating potential competitors, one must consider all close variants of current competitors; such variants arise repeatedly by genetic recombination and mutation.

(3) Risk management differs notably between wild and cultivated growth. Farmers desire all the seeds of a crop to germinate at once; breeders have in response bred out the natural spread in germination times that ensures a persistent seed bank. The seed bank is crucial in wild growth if the current year's growth is wiped out after germination by adverse weather or the like. Likewise, people have bred out many of the chemicals in plants that protected the plants against pests and diseases, because these chemicals were toxic or unsavory to people as well. The burden of crop protection has been in good part externalized to the farmer.

(4) The environment where a crop cultivar is used does not match (any of) the diverse environments of origin of the wild races whose genes were blended to develop the cultivar. Among other things, inherited photoperiod controls are frequently inappropriate in the new environment (Vince-Prue and Cockshull, 1981). Many other mismatches are undoubtedly not even suspected yet.

(5) The value of reproduction may be extensively replaced by unrelated values. Thus, maize has been bred for reproductive *mass*, but now it is almost unable to reseed itself, its seed dispersal capability having been bred out. Even more dramatic shifts in values or objective functions have been made. Many crops are cultivated for their secondary metabolites such as oils or alkaloids. Goals have also been extensively diluted and compromised with corollary goals: uniformity of maturation time, aesthetically chosen coloration and texture, earliness to market, ease of mechanical harvesting, and even *inability* to breed true (so that hybrids remain proprietary).

The above considerations dictate that our objective function for crop optimization must be very specific for the crop and geographic location, and that there may be only weak overlap with the goals of wild growth. However, it behooves us to examine current function in crop cultivars to find deployments of suboptimal strategies that are carryovers from natural selection in wild growth and are suboptimal for agriculture.

C. The Abiotic Environment: Plant Autecology

For the moment, let us view resources by themselves, as having measures of availability that are simply external givens. In this view, resources such as soil water are made available to the plant or else lost (respectively by rainfall and percolation to depth, for example) by processes that have no 'goals' of their own that may conflict with the plant's goals. The processes do not respond in any special fashion to the plant's presence and the plant's uptake of resources. In reality, the availability of any resource is determined in an interactive fashion, wherein competing neighbor plants, animal consumers, and soil microbes all respond to the resource use by the plant we are study-ing. The responses may be made directly to current resource status, or they may be evolutionarily fixed patterns. Thus the other biota fulfill their own goals, frequently interfering with the plant in question in order to divert the resources to themselves. We will defer most considerations of biotic interac-tions until Sec. 1.J.

(i) Resources

Plants use a mulitplicity of resources – minerals, water, carbon dioxide, pho-tons – and must compromise or balance the uses of all of them. The material resources and, to some extent the photons, have several important descriptors:
　　(1) Intensive factors, or concentrations. Two simple examples are the soil water content by volume and the nitrate concentration in the soil solution. Even photons have a useful intensive factor, the photosynthetic photon flux density (PPFD). Intensive factors largely determine the metabolic cost of acquiring a unit mass (or a mole) of a given resource. The more dilute the mineral nutrients are, the greater is the root mass required to extract a gram of nutrient per day. The less intense the PPFD, the greater is the leaf area required to photosynthesize a gram of sugar per day. Intensive factors vary widely: the same species of plant may grow in soils varying a thousandfold in the concentration of a given nutrient, and the ratios of the concentrations of two mineral nutrients may vary by a yet larger factor. The need to cope with this exceptional variation uniquely contrasts plants with animals, whose diets vary only severalfold in fraction as protein or water content or other factors. Plants are sedentary and cannot move to an area that matches very restrictive 'dietary' needs. Instead, plants exploit their impressive plasticity of develop-ment and internal resource allocation (Harper, 1977), as by varying their root:shoot mass ratio or branching pattern or number of organs such as leaves. The corresponding plasticity in animals is largely behavioral; their relative body part sizes and numbers are almost invariant.
　　(2) Extensive factors. For minerals and water, the extensive factor is the soil volume available to the plant, as limited by the plant's own incomplete

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