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Recommendations of the Workshop on the Future Development of Plant Physiological Ecology.[1]

Recommendations Summary

A workshop was held 10–13 December 1984, at Asilomar, California, to consider the progress in and the future development of plant physiological ecology. As a result of that workshop and to further guide the development within the field, a number of observations and recommendations are made. These are clearly noted within the body of the text by *italics*.

Several important summary points can be distilled from the observations and recommendations and these are:

Process studies.—Plant physiological ecology has developed rapidly in the 1960's and 1970's; it is a discipline which continues to develop vigorously in the 1980's with no asymptote in development within sight. Among the rapidly expanding areas are integrated studies of multiple resource interactions (such as carbon, water, and nutrient balances), of the consequences of multiple biotic and abiotic stresses on plant performance, of the factors controlling belowground processes, and of the controls on phenological programming. While most past studies have focused on the single leaf level and then extrapolated to the whole plant and ecosystem, it is clear that more information is needed on the integration of activities at the whole-plant level beyond potted plant observations, and more attention should be paid to the errors involved in extrapolation of leaf-level phenomena to whole plants and plant assemblages.

Discipline interactions.—Because of its integrating approach, physiological ecology can and will continue to have strong and productive interactions with other disciplines. These connections are established with ecosystem and metabolic biology and will likely become stronger with agriculture, forestry, and pollution science. The tools are now becoming available to allow determination of the molecular basis of tolerance and adaptation to various abiotic stresses, setting the stage for strong collaboration of molecular biologists and physiological ecologists. Better integration of physiological ecology and population biology will be necessary to understand such areas as the extent of genetic variation in physiological parameters and its effect on plant performance and population structure.

Supporting facilities.—In the area of research facilities and equipment, it is essential to consider the development of multiuser regionally centered facilities for handling large, expensive pieces of equipment (such as stable isotope mass spectrometers), which are becoming increasingly powerful tools in physiological ecology, yet which may not be justified for individual laboratories. More so than in any other area of ecology, physiological ecology is heavily instrument dependent. Provision for adequate instrumentation funding is essential for its continued development.

Workshop Purpose and Structure

The modern development of plant physiological ecology dates from the 1950's. During the past two decades, in particular, there has been a remarkable growth of this field. This growth has been due to a number of factors, such as: (1) technological advancements (for example, infrared gas analyzers and porometers which have made possible the precise measurement of plant performance under natural conditions), (2) the development of theory (such as energy balance), (3) the excitement of developing answers to such old questions as the physiological basis of the dissimilar behavior of warm and cool season grasses (C_3 vs. C_4), evergreen vs. deciduous species, and of successional vs. climax species, (4) the realization that knowledge of

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the physiological traits of wild plants that grow in nutrient- and water-limited habitats has potential application to agriculture and forestry, (5) the inspirational leadership and teaching of such pioneers as W. D. Billings, and, most important, and due to such leadership, the attraction to the field of an outstanding group of young scientists.

The purpose of the workshop was to review briefly progress in this field, to establish priorities for future research, and to determine what resources are needed to attain these goals.

The products of this workshop are (1) this summary report of research recommendations and priorities, and (2) a series of companion articles to be published simultaneously in *BioScience* that capture the progress and priorities for the future of plant physiological ecology.

Approaches to Plant Physiological Ecology

Physiological ecology, by its nature, is at the interface of ecology and physiology. On the one hand it is concerned with the mechanisms of adaptation to the environment and seeks answers concerning the underlying physiological role of specific mechanisms in the survival and productivity of plants in their natural environment. This is the reductionist aspect of physiological ecology and the one where there have been perhaps the most notable successes. Examples of this are the mechanisms of adaptation to specific environmental factors, such as temperature and light and C_3 and C_4 photosynthesis, where there is a growing understanding of events and their consequences from the biochemical to the physiological and whole-plant performance level. Physiological ecology has, however, a more synthetic aspect as well. In this it is concerned with the population, community, and evolutionary consequences of biochemical, physiological and morphological attributes. Successes have been fewer in this direction, largely because of the difficulty of scaling up from individual leaves, plants, etc., to populations and communities, and because of the time scales involved. Nevertheless, this is an especially important direction for physiological ecology and one which ties the field to other areas in ecology and population biology.

Physiological ecology is concerned with the diversity of responses to natural environments. Historically, much of the effort has focused on severe environments, such as tundra and deserts, where spectacular adaptations to severe stresses are often evident. More recently, physiological ecology is beginning to have an impact in other environments, such as tropical forests where the physical environmental stresses are less obvious (although by no means absent), but biological interactions are much more apparent. Through this broad approach, many insights have been gained that would not have been possible with a more narrow focus on a few species or a few ecosystems.

The alternative approach, selection of one or a few species for intensive study, has played less of a role in physiological ecology than in plant physiology. Only a few examples for woody plants, such as representatives in the genera *Atriplex, Malus, Picea,* and *Pinus,* exist where there have been sufficient studies focusing on different aspects of physiological ecology to lead to a synthesis. However, as we proceed to more complex questions involving resource interactions or the significance of physiological responses in population- or community-level responses, selection of key species for study will become more important. This will be especially true as these complex questions demand more of a team approach, involving population ecologists, physiological ecologists, and others working together.

Future Research Needs in Plant Physiological Ecology

This section is based on the individual papers presented and discussions held during the workshop. It is structured so as to evaluate functional areas within physiological ecology.

Carbon, nutrient and water balance.—Perhaps more than in any other area, the greatest development of plant physiological ecology has been in the area of plant carbon, nutrient, and water balances (acquisition, utilization, storage, and loss). Within the area of carbon balance, carbon acquisition studies have received considerable attention. For terrestrial systems there has been significant progress in understanding pathways of carbon gain, seasonality, and duration of carbon gain by individual leaves, and in the tolerance of leaves to individual abiotic stresses. However, relatively *little attention has been focused on the role of structures other than leaves (such as stems and reproductive tissues) to carbon gain/balance.* In addition, few studies have addressed more integrated aspects of carbon gain. For instance, *little is known about how leaf aging and stresses interact, nor on relationships between whole-plant vs. single-leaf responses to an abiotic stress or stresses.* Previous studies have focused on carbon-gain responses to a single stress; *studies of the more natural phenomenon of multiple stress interactions have not yet been conducted but need to be considered.*

Much less is known about carbon gain by aquatic higher plants, where there is ample reason to suspect that new and unexplored variations in photosynthetic and photorespiratory behavior may exist.

A substantial amount of the carbon in the overall carbon balance is utilized in respiration (up to one-third of the total net photosynthetic gain). In recent years we have come to realize that respiration is not just an undesirable process that results in carbon loss from the plant, but rather a highly regulated process reflecting tissue demands for ATP. Maintenance respiration costs are substantially different from construction respiration costs. *Respiratory metabolism of root tissues and turnover of root carbohydrates are poorly understood for aerobic conditions, and even less for anaerobic conditions.* Unfortunately we have few experimental data on the total respiratory costs for any species (native or cultivated), and little data are available on the environmental dependence of these costs. As a consequence, we find that although we have made significant progress in understanding photosynthetic response to an environmental stress, *we have very little knowledge about the extent of maintenance and repair respiratory costs of the photosynthetic machinery associated with that environmental stress.*

Carbon gain over time is dependent on the fraction of the carbon and nutrients that are allocated to new photosynthetic tissues. Indeed, the *allocation pattern may be as important in determining productivity as is the photosynthetic performance at the leaf level.* It is in this area that our understanding is perhaps weakest. Although crop physiologists have made considerable efforts to elucidate the mechanism of assimilate transport and partitioning, the understanding of these processes is still rudimentary and limited to a few cultivated species. *Future research in physiological ecology must include efforts to answer the question of how ecologically different species allocate carbon and nutrients to primary plant functions and how this allocation is influenced over time by major environmental factors.*

The linkage between photosynthetic and water relations activities via gas exchange processes which are mediated by stomates is fundamental in understanding plant adaptation. Water relations and transpiration to the relatively dry aerial environment play a central role in determining the geographical distributions of plants. Although progress has been made in modeling and understanding the photosynthetic process, we are still at the stage where *it is possible to simulate water loss and its control only with empirical models but not from an understanding of the mechanisms involved.*

The linkage of transpiration and photosynthetic studies in physiological ecology and the recognition that stomats simultaneously regulate the rates of gas exchange of both processes has led to progress in understanding leaf-level patterns observed in the field. However, as with photosynthetic studies, *too little effort has been made to link leaf-level observations with whole-plant responses.* Too little information is available on the growth constraints imposed on and responses of whole plants to limited water availability or to variable evaporative demand vs. the more easily measured leaf-level responses. This linkage must get stronger if we are to understand the constraints imposed by stresses and the adaptive significance of plant responses to those stresses.

Many of the questions regarding unknowns controlling carbon allocation also extend to water relations. That is, the roles of hormones or other signals as controls for transpiration, leaf conductance, or water potential and in controlling growth processes are poorly understood for wild plants. Although this area has received attention by crop physiologists, insufficient data are available for any species to put together a coherent mechanistic picture.

Interest by physiological ecologists in the

United States in plant nutrition is relatively recent, reflecting perhaps a preoccupation with light, water, and temperature as more obvious abiotic stresses. Although still in its infancy, short-term studies of direct nutrient uptake by intact plants are indicating that both environmental and plant variables have a significant impact on uptake rates, and that these rates may be several orders of magnitude higher than previous estimates based on whole-plant budgets. Simulation modeling clearly indicates that nutrient depletion zones will form around individual absorbing root surfaces, but *the relationships between diffusion, uptake, root spacing, and depletion are poorly understood at present.*

Linkages between nutrient uptake and use with carbon balance studies are rarely made, yet it seems clear that these factors do not act independently. *Future studies should consider the interactions of water, carbon, and nutrient balances and the constraints imposed by environmental factors on the allocation of these components.* At present little is known about the nature of nutrient storage in wild plants. Until recently, little attention has been given to nutrient loss from a physiological standpoint, although it may be just as important as uptake to the nutrient budget of a perennial plant. *Controls over nutrient retranslocation, especially in regard to changes in photosynthetic activity or environmental stresses (e.g., water stress and herbivory) are not understood,* and few controlled studies have addressed these questions.

Plant architecture.—Plant physiological ecology has primarily focused on functional aspects. Although structure is intrinsically coupled with function, there has been more emphasis on investigating physiological traits than on the functional significance of plant architecture. This is not to say that architecture has been overlooked, since some aspects of shoot structure have been reasonably well investigated, particularly those that relate to light interception and photosynthesis. To a lesser extent, branching patterns, structural dynamics, elastic buckling properties, and hydraulics have also been investigated.

Architecture places constraints on the morphological flexibility of shoot systems with respect to filling unfilled gaps in a canopy, to the apportionment and utilization of assimilates, and to recovery from herbivory. This area has received little research attention at the ecophysiological level thus far, but should be an overriding consideration in an analysis of adaptation.

The functional significance of root system structure has gone little beyond the stage of describing root system morphology. Technical limitations presently impose a barrier to the kind of detailed experimentation that can be conducted on aboveground plant parts. Analyses of root system branching patterns are still only in their infancy, and *the relationships between root system architecture, metabolism, and soil resource exploitation are poorly understood.* Assessment of the functional implications of root system architecture should receive more attention. *Little is also known about competition for belowground resources.* Favorable aboveground nutrient-use efficiencies may not correlate well with success in competition for belowground resources. Again, this area is virtually untouched. Unlike the new technical advances for assessing shoot-system architecture, few advances have been made for assessment of belowground architecture. The use of NMR, high-energy radioactive isotopes, and x-ray tomography may be technical advances on the horizon, but for the near future the approaches will probably continue to be tedious, expensive, and inexact. Still, the questions are no less pressing.

Plant architecture also involves the manner in which foliage elements of different age and physiological activity are positioned in different microenvironments. Thus, *architecture must be considered when scaling up the results of single-leaf measurements to the whole-plant level.* Depending on the plant architecture, this can be a formidable sampling problem, and the results from single leaves may not provide the same perspective as from measurements of whole-plant gas exchange. The importance of gas exchange measurements of whole plants or larger subunits of plants under field conditions still needs to be emphasized.

Plant architecture studies can also serve as a vehicle to force whole-plant perspectives in physiological ecology. Recent advances at the single-leaf and individual-root levels have been impressive, but a view of whole-plant function is lagging. Too often, unfortunately, research of whole-plant function has only meant studies of whole plants in pots. What is needed are data on whole-plant performance under field conditions.

Stress tolerance.—Whether they are climatological (such as light, temperature, and humidity), biological (such as insects and pathogens), or edaphic (such as extremes in water and minerals), environmental stresses play a primary role in determining the distributional ranges of plants. Although in some cases a single factor seems to correlate well with the success of a plant, the basis for that success may be very complex. The classical studies of ecological races by Clausen, Keck, and Hiesey confirm the complex nature of adaptation in altitudinal races and show that many genes are involved in the determination of such characters as frost tolerance or time of flowering. The prospect of establishing physiological and genetic bases for plant adaptation that was first developed in this classic series of transplant experiments remains largely unrealized as an important goal of physiological ecology. *For many stresses, an understanding of the mechanistic basis of tolerance will come from studies of whole-organism integrated responses in addition to those at the cellular and subcellular levels.* Recent advances in subcellular physiology and in molecular biology may provide important new tools. *Specific gene products and the corresponding genes that confer stress-tolerant characteristics can now (at least in theory) be identified, and such approaches could complement more traditional approaches.* Such approaches appear to be providing new insights into adaptation to heavy metal tolerance and chilling and freezing tolerance, to name a few, and will likely continue to provide new insights in the future. While a number of important stress adaptation mechanisms can be perceived at the molecular level, they are generally integrated with responses of the morphological, developmental and phenological levels. A dissection of these integrated chains of response has not generally been made.

There is a need for parallel development of physiological and biochemical studies on the basis of stress tolerance. The need for rapid and reliable quantitative methods cannot be overemphasized. While many of these methods will be laboratory-based initially, there should be encouragement to develop field-portable techniques where appropriate.

The recent changes in subcellular physiology and molecular biology hold promise for determining many of the mechanisms for stress tolerance. These are techniques, but not a roadmap. *Plant physiological ecology as a discipline should not stand apart from a trend involving molecular biology approaches.*

Reproductive physiology.—In recent years, there has been an interest in understanding the role of reproductive structures in terms of carbon and nutrient balances and of understanding the costs associated with reproduction. Although these studies are just now becoming more common, a number of interesting and important observations have already been made and there is the suggestion that this may be an extremely important area for future ecophysiological research. *Plant reproductive ecology requires the joint application of the approaches of demography, population genetics, and physiological ecology.* Thus, this is one of the subfields that interacts directly with the interests of closely aligned ecological subdisciplines, providing a bridge between them.

Photosynthetic measurements on reproductive structures have refuted the old idea that such structures were strictly carbon sinks, and that reproductive allocation could be accurately estimated by measuring only the fractional biomass of the reproductive structures. Carbon gain by the reproductive structure is both species and time dependent, but with the preliminary knowledge available, it is not yet clear why this variation should occur. Nor is there much information on the nutrient constraints imposed on growth in other plant parts when a reproductive event is initiated. The total respiration costs for reproduction are also unclear; no studies have yet attempted to separate maintenance and growth respiration costs, nor to estimate the extent to which respiratory carbon dioxide is internally recycled.

As is the case with carbon balance studies, there is also *little information available to evaluate the costs and tradeoffs between reproductive and vegetative growth.* We cannot separate hormonal control from carbon and nutrient limitations on the timing of reproduction and on the quantity and quality of the progeny produced, on the basis of present knowledge.

Seedling establishment is a critical phase of the plant's life cycle, and seed quality is an important factor affecting the rate of establishment. Thus, *an understanding of mineral and carbon nutrition of reproductive structures and of the genotypic variation and plasticity associated with the quality of seeds produced may provide new insights into one very important aspect of plant fitness and population structure.*

Herbivore defense.—Although historically, the area of herbivore defense has been investigated primarily by biochemists at one end of the spectrum and ecologists at the other end, it now appears that physiological ecology approaches are beginning to have a significant impact on this field. *The notion of costs and constraints associated with carbon/nutrient allocation to herbivore defense vs. allocation to other plant function has provided new insights into why plant behaviors may differ between species, and why an individual plant may changes its antiherbivore behavior through time and with change in resource levels.* As our estimates improve for carbon/nutrient balances of individual plants, and for the production cost and turnover rates of different herbivore-deterrent compounds, this area of investigation will continue to be productive.

The Interface of Plant Physiological Ecology and Related Disciplines

The interaction of plant physiological ecology with other disciplines is an exciting frontier. Study of the mechanisms of environmental adaptation permits physiological ecologists to interact with investigators of ecosystems and population/community ecology, and of molecular and metabolic biology and population genetics. Physiological ecology as a basic science can also forge strong linkages with more applied studies such as crop and forest physiology and pollution-related biology.

Molecular and metabolic biology.—There appear to be unlimited opportunities for making connections between physiological plant ecology and molecular and metabolic biology. *A great deal of the recent progress in physiological ecology has been at the metabolic level, and this trend is likely to continue in the future.* Despite this progress, however, there have been few satisfactory explanations in either molecular or metabolic terms for any of the significant interactions between plant species and their environment, nor have the metabolic success stories been integrated to explain ecological processes such as plant performance, survival, and distribution.

While the possibility of utilizing molecular genetics to isolate specific genetic elements is exciting, the principal obstacle remains the identification and cloning of the gene complexes associated with key physiological processes. These tend to be whole organism rather than single gene processes. However, some discrete systems can be targeted. In a related area, plant physiological ecology has yet to take much advantage of modern genetic techniques or to follow through on the pioneering studies of ecotypic differentiation. *There is evidence available now to show that molecular genetic techniques can provide such insights and that this would be a fruitful approach for integration of ecophysiologists, population biologists, and molecular geneticists.*

Population and community ecology.—Population biology and community ecology are disciplines closely aligned with physiological ecology, *but the interactions between these fields and physiological ecology have been few thus far and slow to develop.* While physiological ecologists are often most interested in mechanisms of adaptation and interaction with abiotic/biotic factors, population biologists and community ecologists are interested in the interactions between different genotypes and with stages of the life cycle for a species, or in the interactions between different species within a community. Connections between these fields are essential if we are to understand the role of genotypic variability in determining plant success or of the constraints imposed by physiological limitations to the higher interactions among plants.

The apparent lack of interaction between physiological ecology and population biology is without justification. While a population biologist may more easily perceive a resource in terms of "safe sites," whereas a physiological ecologist may measure the absolute concentration of that resource, the true problem is more likely that each lacks a working knowledge of the other's science. Physiological ecologists have historically been process oriented (usually at the single leaf level) and have too infrequently extended their studies from the process to the whole plant through reproductive cycle levels. Studies of genetic variation or of ecotypic variation by physiological ecologists are becoming more common, but for the last 20 years have been minimal. In contrast, population biologists often perceive that detailed studies involving heavy instrumentation are unnecessary when they wish to know the consequences of a behavior, or that behavior differences exist. Reality lies somewhere between the extremes. Biochemical, physiological, and morphological characteristics which are studied in physiological ecology impose constraints on the types of interactions between organisms and on the timing of these interactions. Future studies must provide for greater integration of these two fields.

Ecosystem ecology.—Past studies of plant physiological ecology in the United States have been highly comparative with much information accumulated on adaptive modes of various growth forms within a given community, as well as for given growth forms among community types. A recent book (*Physiological Ecology of North American Plant Communities*) summarizes this knowledge. Such information was amplified and integrated into an ecosystem context during the International Biological Program. Unfortunately, for largely historical reasons, we have detailed knowledge of resource control of plants of certain ecosystem types, e.g., arctic-alpine, desert, chaparral, etc., but limited information on plants of certain ecosystems of economic or biospheric importance, such as many temperate and tropical forest types.

It is becoming more widely recognized that key species within the ecosystem can have a dominant effect on controlling rates of transfer processes in ecosystems. This is most apparent in nutrient cycling studies, and it is in this area that physiological ecology and microbial ecology may best integrate. That is, the control of nutrient availability to the primary producers will be affected by key higher plant processes as well as by the interactions with microbes. At present we have little information available to understand the types and role of genetically based physiological diversity/tolerance differences in microbes. Ecosystem management studies indicate that significant progress can be made when the reproductive and physiological traits of the controlling species are understood; the integration of physiological ecology approaches to ecosystem studies is likely to continue to be very successful.

Agriculture and forestry.—Physiological ecologists and agricultural physiologists basically work on the same kinds of problems. The separation of interests is artificial, based on the kinds of organisms investigated (generally wild vs. cultivated species), and in most academic institutions on the separation between basic biology and agriculture departments or colleges. Although these divisions are likely to remain, much can be learned from increased interactions between these two disciplines. Physiological ecology stands to gain because a diversity of purebred lines is available for many species; these resources allow one to ask a number of questions that cannot yet be asked of the genetically diverse native plant systems. Agricultural sciences will benefit from exposure to plant physiological ecology, because wild plants offer much greater extremes in stress tolerances than can be found in currently cultivated plants. This is a rich resource for understanding fundamental limitations to crop improvement as well as being a potential new source of genetic material.

Increased interactions are most likely to arise from individual efforts to cross-link the disciplines and efforts to publish results in the other's journals.

Pollution biology.—Plant physiological ecology and ecophysiological approaches can and currently are contributing significantly to our understanding of the impact of air pollutants and plant tolerance. Gas exchange studies have provided mechanistic explanations for air-pollution-caused growth reductions in the absence of visible leaf injury, and these results have shown that leaves and individual plants, as well as species, may vary in their capacity to absorb air pollutants without detrimental physiological effects. Stomatal behavior is a key component, since the stomata regulate gas exchange between the leaf and its environment.

Plant physiological ecology approaches are likely to contribute to an understanding of air pollution effects in several key areas: (1) interaction of rain with the foliar surface, and with the rhizosphere, (2) the biochemical and physiological mechanisms whereby pollutants within the leaf affect metabolic processes, (3) the impact of a pollutant in the context of other natural stresses, and the consequences of these stresses in combination, as occurs under field conditions, and (4) genetically based variability in sensitivity to air pollutants.

Equipment Needs in Plant Physiological Ecology

There is an inherent need for rugged and precise equipment in physiological ecology. Historically, technical advances in areas such as infrared gas analysis (for carbon dioxide determinations) and porometry (for measuring water loss) allowed precise measurement of plant performance that resulted in substantial progress in the field. *There continues to be substantial need for equipment if progress in physiological ecology is to be sustained.* New techniques now under development will allow us to determine the metabolic and molecular details of the exact mechanisms of adaptation. These techniques, however, are often expensive.

Equipment limitations within physiological ecology have two origins. First, research support is limited, and competition for it is keen. Second, appropriate instruments have not always been available and therefore scientists have often needed to develop them before research advances could be made. Traditionally, the ecological sciences have not relied on expensive equipment. Physiological ecology, however, is an exception that arises from the need to measure/control a number of factors that interact with the process of interest, the need to grow plants under controlled environments, and the need to bring modern instrumentation equipment into the field. In the past, much of the equipment was borrowed from other discplines and often adapted for uses quite different from that originally intended. Moreover, there was a great reliance on construction or assembly of equipment by physiological ecologists for their specific needs. Only recently has the field grown to a size to allow commercial development of specialized instruments tailored to the needs of physiological ecologists. Most of these instruments are still being developed by individual physiological ecologists, but their commercialization is greatly increasing their availability to others. As a consequence, new instruments are much more rapidly adopted today.

The ongoing revolution in electronics has dramatically changed our abilities to measure resource levels and flux rates, and is a major factor in the dramatic improvement of instruments. Microelectronic developments have resulted in data acquisition and data resolution capabilities that provide a measurement and statistical sophistication impossible 10 years ago. The low power requirements, miniaturization, and autocalibration afforded by microprocessor-based systems have allowed development of field-portable equipment with good resolving power and control capabilities. Instruments such as the new null-balance photosynthetic systems give a level of complexity for field measurements previously available only in the best laboratory-based systems. The ability to perform these field measurements is providing many new insights into the functioning of plants in their natural settings and in experimentally manipulated field environments. The inexpensiveness and versatility of this equipment provides for a relatively large return. For example, the portable photosynthesis systems can move easily between field and controlled-environment laboratory studies.

Another area where advances in microelectronics have greatly increased our capabilities is in microprocessor-based data acquisition systems and on-line data reduction. These systems allow for much more detailed and precise measurements of environmental parameters and are very inexpensive. When the labor savings due to the on-line data reduction capabilities are considered, these systems have significantly reduced the costs per measurement and have increased the reliability of the resulting data. Moreover, the ability to do real-time computations of physiological rates, etc., allows for much more accurate and reliable control and manipulation during experiments than previously possible. As we move towards answering more complex questions, it will be necessary to give high priority to updating older equipment to microprocessor-based automated systems.

The recent advances in metabolic and molecular biology, and the interfacing of physiological ecology with these approaches, will require a heavy investment in equipment, or *at least access to such equipment.* For example, in vivo measurement of high-energy phosphate pools using NMR is now possible, and could conceivably be used to measure the energy status of plants in different environmental conditions. Careful consideration needs to be given to how development costs could be met, and ultimately to how such equipment will be utilized. The costs will no doubt need to be shared between investigators and projects, perhaps cutting across disciplines. Studies with carbon-11 face a similar problem. Its utility in understanding short-term patterns of carbon allocation has been well demonstrated, but the high costs have limited its application.

Large-scale instrumentation is nevertheless having and will continue to have a significant impact in physiological ecology. These laboratory-based equipment needs include elemental analyzers and scanning electron microprobe systems, as well as specialized analytical equipment for determining tissue ion and biochemical compositions. Stable isotope analysis shows great promise for investigating plant/environmental, plant/soil, and plant/herbivore interactions. Previously, analysis of carbon isotope ratios has played a key role in understanding the distribution of C_3, C_4, and CAM pathways of photosynthesis. Recent developments, however, show that stable isotopes can be used for understanding many other processes, including transfer rates as well as integrated responses. Carbon isotope measurements, for example, are a sensitive indicator of the integrated water use efficiency of a plant, and nitrogen isotope measures can distinguish between sources of nitrogen (N-fixation vs. nitrate uptake). The utility of other stable isotopes of oxygen, sulfur, and hydrogen is just now being explored. Stable isotope mass spectrometry initially developed in the geological sciences because of interests in variations in the natural abundance of elements and the isotopic enrichments present in various pools. Expansion into the medical sciences occurred because of its utility in tracer studies using natural abundances, or with enriched labeling, as an alternative to radioactive isotopes. The development of stable isotope mass spectrometry in physiological ecology is quite young and its expansion is very much limited by equipment availability (approximately 85% of the equipment is in geochemical sciences, 10% in the medical sciences, and the remainder scattered throughout a diversity of fields).

The capacity to grow plants under defined conditions is highly important to physiological ecology. Most laboratories have access to growth chambers, but these often have inadequate lighting and poor environmental control. In many experiments glasshouses are used to overcome some of the limitations, even though the level of control is even poorer. Phytotrons such as the Duke University Phytotron serve as regional facilities and are a valuable alternative to maintaining expensive growth facilities for each laboratory. An important advantage of phytotrons is the ability to replicate experiments in different chambers to remove chamber effects. Thus phytotrons allow for the statistical identification of much more subtle differences between species or treatments than is otherwise possible. The major disadvantages of current phytotrons is their distance from the laboratories of many investigators, and the need for growth facilities to be in sunnier locations to create natural irradiances more carefully. For this reason growth chambers in the investigator's laboratory will continue to play an important role, particularly where other specialized instrumentation needs to be close at hand. Thus, attention needs to be given to improving the designs of growth chambers and identifying the sources of variability within and between them.

A closely related problem is the control and manipulation of plant growth in the field. For many types of studies, it is inappropriate to bring seedlings or relatively small plants into a growth chamber. Instead, it may be more appropriate to move the controlled environment to the field. This has been done, for example, by using clear plastic chambers in order to study CO_2 effects on arctic tundra plants. Large but portable chambers of this general type will become increasingly important as we attempt to scale up our understanding from single leaf processes to population and community levels.

The large-scale instrumentation required for the future in physiological ecology will increase the expense, and careful consideration of how to fund it and make it available will be required. In some instances, regional-

ized or national centers may be a sensible approach. Careful study of the cost effectiveness on a case-by-case basis will be required. It should be pointed out that investigators will need access to instrumentation for development of the techniques in addition to later use for solving specific research problems. The development is an essential step in opening up new research avenues, but one that is often difficult to carry out. On a smaller scale, cooperation between investigators and instrument manufacturers will also aid in making equipment more readily available and functional, and should be encouraged. Mechanisms to promote industry/scientist cooperation could significantly enhance research progress through development of new sensors and instruments.

Other Factors Bearing on the Development of Plant Physiological Ecology

Plant physiological ecology is a rapidly emerging discipline making significant new contributions to our understanding of fundamental biological processes. Future growth in this field will be dependent on a number of factors. Financial resources, to be sure, will have an important impact, but beyond this there are a number of other factors to be considered.

Job opportunities.—Much of the current research in plant physiological ecology occurs at academic institutions. With the limitations being placed on the growth of academic endeavors in general, this limitation can restrict development of the field. This restriction is coming at a time when the discoveries from plant physiological ecology are beginning to have a significant impact on ecosystem management, in the agricultural sciences in general, and on specific concerns about the need to consider the significance of genetic manipulations in a whole-plant context, an approach which characterizes plant physiological ecology.

The job market will limit growth in the academic area, but beyond that there is considerable room for expansion in physiological ecology. Inherent in plant physiological ecology is an experimental approach involving analyses of diverse plant features, functions and adaptations at the whole plant level. As such, it is an approach readily adaptable to fundamental problems in agriculture, forestry, and air pollution biology.

Biotechnology.—Biotechnology is currently a strongly emerging field. However, it is not a discipline, but rather a suite of techniques that can be used to answer various research questions. As such, plant physiological ecologists should become actively involved in interactions with this field, as it is likely to provide the necessary tools for answering a number of fundamental problems of ecological interest. At the same time, it is likely that the overall significance of products derived from biotechnology will not be answerable by molecular biologists, but will require collaborative efforts with whole-plant approaches. The physiological ecologist must provide information and perspective on whole-plant traits that are most worthy of the biotechnologist's efforts. For example, improved characteristics of one enzyme may be wasted effort if other constraints are more limiting for plant performance. The choice seems to be whether physiological ecologists will wish to interact with the new molecular biology and its tools, or whether molecular biologists will have to get involved in whole-plant performance analyses on their own.

Publications.—Plant physiological ecology historically has developed from the field of ecology, and the closest affiliations lie here, as opposed to plant physiology. Publication and transfer of research results is an important aspect affecting the growth of a field, and the awareness of others outside the field about the progress being made. This field is moving rapidly, and getting information out and into the open literature is important. There is a bottleneck, because most of the ecologically oriented journals (such as *Ecology* and *Journal of Ecology*) have long turnaround times (about 18–24 months), as opposed to journals in the fields of chemistry, molecular biology, and plant physiology, which typically have turnaround times of 3–10 months. The solution to this problem is not clear at present. One possible solution is to add a new journal, oriented specifically to plant physiological ecology (to some extent *Oecologia* serves this function). A second and perhaps more feasible solution is to increase the size or frequency of the currently utilized ecological journals, but this suggestion seems not to be acceptable to the respective societies. Although this concern is not of direct interest to the National Science Foundation, it has indirect bearing on NSF and the grants it provides to investigators. This is obviously because progress in the field and dissemination of information obtained from funded research is slowed down.

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