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Lessons learned while extending physiological principles from growth chambers to satellite studies

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Summary Over the last three decades, physiological principles established in laboratory studies have been applied to systems at progressively larger scales and are now firmly merged into the fields of ecology, ecosystem modeling, forest protection, and global change research. To expand the vision of any field requires that scientists from different disciplines build a bridge across the chasm that normally exists between the knowledge bases and perspectives of different fields. Bridges are built most quickly when representatives of different disciplines see the possibility of mutual advantage in collaboration and seek to quickly demonstrate that potential. Usually, however, the process is laborious because approaches and techniques must be modified to address problems at a different level of integration. Successful bridge builders have, almost without exception, established credibility in their own field and have then identified a kindred spirit with similar credentials in another. They usually establish a pilot study that involves apprentices as well as established scientists. If the approach is successful, the younger members of the team often take the lead in further advancements. Managers of large centralized programs should foster interdisciplinary exchange, particularly at times when advancement in one field languishes. To expand collaboration, it is often necessary for scientists to seek common properties that simplify relations across a wide range of biological and physical conditions. This integrative perspective is essential and is fostered by participating in cross-disciplinary workshops and conferences and by reading outside one's field.

Keywords: cross-disciplinary research, integrated research, research management, tree physiological research history.

Introduction

Looking back over a span of more than three decades, I am amazed how insights and approaches developed in laboratories by physiologists have slowly been incorporated, through collaboration with other disciplines, to reach the scope required for the analysis of global change. It is my privilege to have participated in this scaling exercise, and along the way to have learned some lessons. Jumping across the chasm between disciplines is a dangerous pursuit, and requires more preparation and dependence on others than I originally envisioned. Building a permanent bridge between disciplines is a particularly slow process, best achieved when founded on sound principles and initiated from both sides. The first bridgehead, to be sound, must be established with a joint commitment to test an idea that has benefits for all involved.

In atonement for periodic expeditions away from my physiological base, I agreed to share some personal experiences before an international audience of physiological ecologists who attended an International Union of Forestry Research Organizations workshop in South Africa that is featured in this journal issue. As my story unfolds, mentors and fellow travelers will be identified and some of their contributions noted. This paper is broken into five sections which represent, more or less, my chronological exposure to the following topics: (1) defining environmental gradients, (2) tree water relations, (3) process modeling, (4) integrated pest management and (5) global change research. This range of topics may appear unrelated, but underlying them is a common philosophy and approach to collaboration.

Defining environmental gradients

Plant geographers, starting with von Humboldt in 1807, appreciated the advantage gained by observing as wide a range of conditions as possible before attempting to generalize. Following this approach, they noted that the distribution of major life forms, rather than taxonomic groups, was related to the general climate. Ecologists working in specific regions developed elaborate classification schemes to relate the distribution of local flora to various physiographic features (slope, aspect, soil type) as well as to general climatic conditions. Some ecologists interpreted the spatial distribution of various species as representing different sectors of environmental scales in moisture, light, temperature, and soil fertility (Ramensky 1930, Ellenberg 1956, Bakuzis 1969). There was concern, however, about how to quantify these environmental scales more functionally (Mason and Langenheim 1957).

In 1959, when I came to the University of California at Berkeley from the University of Minnesota, I had been steeped in the literature and approaches of European and North American ecologists under the guidance of two great scholars, Egolfs Bakuzis and Donald Lawrence. At Berkeley, I was introduced to physiology at a time when many new insights in understanding photosynthesis and the environmental controls on flowering, growth, nutrient uptake, and other processes were unfolding (Levitt 1956, Bassham and Calvin 1957, Went 1957). Facilities in which environmental conditions could be precisely controlled were key to making rapid advancements at that time, and Edward Stone, for whom I was a teaching assistant, had among the best climatically controlled growth rooms then available.

With my forestry background, I knew many ways to manipulate stands of trees and other vegetation, and how to design efficient sampling to meet local objectives. At Berkeley, the emphasis was placed on developing interesting and testable general hypotheses before allowing students to gather empirical data. In the forest ecology course taught by Professor Stone, the scope was clearly global. He made a distinction between the potential (physiological) and actual (ecological) range of a species. Growth room studies by Henry Hellmers had shown that many tree species had different optimum day and nighttime temperatures from those common in their native ranges (Hellmers 1962). Professor Stone's slides of fast-growing plantations of radiata pine in New Zealand brought home the importance of recognizing physiological limits, which applies today when considering the implications of global climatic change.

My Ph.D. dissertation represented my first leap across fields. It was part of a joint project in the coastal redwood region that was under the direction of four outstanding professors: Jack Major (ecology), Edward Stone (physiology), Herbert Baker (taxonomy) and Paul Zinke (soils). Four graduate students, one under the direction of each professor, worked together to accomplish a variety of related goals. My project was to quantify environmental gradients with seasonal measurements of temperature, soil water, light, and growth-room bioassays of soil fertility (Waring and Major 1964). The overlapping distributions of selected representatives of the local flora, identified with the help of James Griffin, a fellow graduate student, confirmed the possibility of using the composition of vegetation to position sites environmentally.

Following graduation, I accepted a position at Oregon State University. My first project was to extend the environmental gradient approach developed in the redwood region to a larger area in northwestern California and southwestern Oregon. In doing this, my graduate students, Chester Youngberg, and I developed more refined physiologically based measures of light (Atzet and Waring 1970), temperature (Cleary and Waring 1969), moisture (Waring and Cleary 1967), and soil fertility gradients (Waring and Youngberg 1972). The analysis of the flora showed that some species occupied different environmental niches in closely associated geographic regions (Waring 1969), whereas endemics maintained their presence in environmentally restricted situations (Waring et al. 1975). These discoveries, although interesting, were frustrating in the sense that competition among species prevented generalizations about the environmental distribution of flora outside of one region. Perhaps physiologically defined environmental gradients had more value in quantifying general physiological processes.

Tree water relations

In the early 1960s, methods to assess plant water relations were restricted mainly to the laboratory. But Ralph Slatyer, a world-class scientist from the Commonwealth Scientific and Industrial Research Organization (CSIRO) in Australia, convinced me when he visited Oregon in 1964 that it was worthwhile to bring samples from the field to the laboratory to determine leaf water potential. Following Dr. Slatyer's suggestion, we collected samples at night and stored them under refrigeration. Although laborious, the underlying soundness of the approach made us receptive to the introduction of the pressure chamber technique (Scholander et al. 1965). Brian Cleary, a graduate student, and I built our own pressure chamber and demonstrated that the distribution of vegetation correlated with measurements of predawn water potential following a long summer drought (Waring and Cleary 1967). Dr. Cleary went on to establish a company (PMS Instruments, Inc., Corvallis, OR) to build pressure chambers, whereas I sought ways to demonstrate applications.

Richard Walker, another mentor of mine at the University of Washington, showed interest in the pressure chamber, and introduced me to Otto Lange (University of Würzburg) and Werner Koch (University of Munich) who were demonstrating climatically controlled cuvettes at the International Botanical Congress held in Seattle in 1969. At that time, I had just arranged for sabbatical leave with Walter Larcher at the University of Innsbruck, so these contacts were immediately valuable in allowing me to expand my interest in field measurement. Professor Koch had installed towers in a spruce forest where he was monitoring photosynthesis and transpiration on selected branches throughout the year. This was my first experience using towers to access tree canopies. The view from the top platform impressed on me the inappropriateness of generalizing from a few branches to an entire forest canopy; another approach was clearly needed. This insight stimulated me to attend a workshop featuring forest micrometeorology that David Ford and Paul Jarvis organized in the United Kingdom in 1976.

While in Europe, I took the opportunity to introduce the pressure chamber to many leading physiologists including Walter Larcher and Walter Tranquillini (Austria), O.L. Lange and E.-D. Schulze (Germany), F.E. Eckardt (France), P.E. Weatherley and P.G. Jarvis (Scotland), L. Leyton (England), P.F. Wareing (Wales), and T. Ingestad and S. Linder (Sweden). Among these scientists I found a common interest in a set of physiological processes that allowed them to appreciate and cite each others work. I also learned the value of having to explain concepts in another language (Waring 1970), and, as a result, I still require my Ph.D. students to speak a foreign tongue.

While on sabbatical in Innsbruck, I presented a series of lectures on modeling in ecology to stimulate interest in this aspect of science, which appeared to be largely lacking in biological research programs throughout Europe. In contrast, the International Biological Program (IBP) in the United States was designed around the premise that system models would be created and tested from data acquired during the

1970s (Reichle 1970, Patten 1971). Returning to Oregon as a site director for the IBP project in the Coniferous Forest Biome (CFB), I was anxious to forge ahead with process modeling.

Process modeling

The IBP provided a unique opportunity for people to cross disciplines. In Oregon alone, the program involved more than 100 people from ten departments plus a cadre of scientists in the U.S. Forest Service Experiment Station led by Jerry Franklin, Deputy Director of the CFB. Our headquarters were in Seattle at the University of Washington, where Richard Walker joined with Leo Fritschen (micrometeorologist) and David Scott (physiological ecologist/silviculturalist), under the leadership of Stan Gessel and Dale Cole (soil scientists) to measure and model annual water, carbon, and nutrient budgets of young and old-growth forests (Waring 1979, Edmonds 1982). In addition to established scientists, the United States component of the IBP supported a large number of post-doctoral people and graduate students. The post-docs were a critical addition because they came from a wide variety of fields and were challenged with a common objective: assembling ecosystem models.

It would seem that supporting large teams of scientists to work on a common project was an ideal way of bridging fields, but the situation was far from perfect. Only conceptual models were available at the start of the IBP. To construct computer simulation models from scratch took more than five years. During that time, a mountain of data accumulated in data banks, but important values, such as leaf area index (LAI) were determined with questionable accuracy (Marshall and Waring 1985). It was also clear that modeling and data gathering were uncoordinated, and this presented a perilous situation for the CFB program.

Professor Walker and I discussed the possibility of bringing in assistance from our overseas contacts. Paul Jarvis agreed on short notice to come for 6 months and to reside in Seattle near the site where photosynthesis and forest energy balance measurements were collected. Ken Reed, a former graduate student with field and modeling experience (Reed and Waring 1974) came to Seattle to work with Paul Jarvis. Together with other scientists at the University of Washington, Reed and Jarvis developed an empirical approach to modeling photosynthesis and transpiration that is still in vogue (Reed et al. 1976, Lloyd et al. 1995).

Improvements in estimating LAI came through attempts to extrapolate measurements of transpiration to steep ground surrounding gauged watersheds at the Oregon IBP site (Edmonds 1982). Jerry Kline, a former classmate at Minnesota, had shown that injection of tritiated water into tropical rain forest trees provided a means of estimating transpiration over periods of a week or more (Kline et al. 1970). We arranged to have ten trees injected at the Washington site and noted that the flux of tritium through the stems was directly related to the cross-sectional area of sapwood (Kline et al. 1976). This finding led to a correlation between sapwood area and leaf area (Grier and Waring 1974, Waring et al. 1982). Accurate estimates of leaf area proved essential to scale gas exchange processes from individual trees to forest stands (Waring et al. 1980), and from forest stands and other vegetation types to watersheds (Waring et al. 1982).

With transpiration and leaf area data in hand, Steve Running, a graduate student, assembled our first physiologically based simulation model (Running et al. 1975). Bill Emmingham, a Ph.D. student, expanded the transpiration model to estimate seasonal variation in photosynthesis at different sites (Emmingham and Waring 1977). To scale to watersheds required that additional components be added to the transpiration model. These additions included water storage in snow, on canopies, and in litter, as well as the lateral transport of water through surface runoff and subsoil seepage to streams. In adding these components to the model I was fortunate to be able to collaborate with two hydrologists, James Rogers and Wayne Swank, United States Forest Service scientists, who had modeling expertise and data available from gauged watersheds in North Carolina and Arizona, which enabled us to demonstrate the generality of a hydrologic model (Waring et al. 1982).

The wider testing of ecosystem models took many years because few ecological or micrometeorological studies measured all the essential variables. Only recently, following advances in remote sensing and in extrapolating climatic data, has it been possible to extend model predictions to a range of sites in Oregon that were originally established by Henry Gholz during the IBP (Gholz 1982, Glassy and Running 1994, Peterson and Waring 1994, Running 1994).

Integrated pest management

Until the 1980s, research in forest protection was largely fragmented into three fields: entomology, pathology, and fire control. Broad applications of pesticides were the common prescription to control insect populations, and to a lesser extent, to restrict the spread of diseases. In 1962, Rachel Carson in her book *Silent Spring* awoke the general public to the dangers of indiscriminate application of pesticides; thus, by the 1980s, forest managers were highly receptive to other approaches. At that time, forest insect and disease outbreaks reached epidemic proportions as a consequence of fire suppression policies throughout the western United States during the previous half century. The general view was that older forests were more susceptible to pests than younger ones, and should therefore be quickly logged. A few silvicultural experiments with thinning suggested alternatives but no formal experiments had been conducted or evidence provided to explain the differential response of thinned and unthinned trees to insect and disease attack.

Bark beetles were then, and still are, among the most feared of forest insects because they kill apparently healthy trees in a single year. By the 1980s, entomologists had obtained many insights into bark beetle population dynamics and discovered how to attract insects with chemicals (pheromones). Because beetles attack under the bark, they were impossible to control through aerial application of pesticides. Gary Pitman, an entomologist from Boyce Thompson Institute, was transferred for 3 years to my department to share insights that might lead to possible silvicultural controls. The timing was perfect: an insect outbreak was in progress, Dr. Pitman had pheromones to attract the insects, and we had a grant from the National Science Foundation that funded a bold silvicultural experiment.

We showed over a 3-year period that old-growth lodgepole pine forests require thinning and fertilization to minimize mortality from bark beetles, a desirable option from clearcutting for both foresters and the public. Our experiment included a treatment designed to extend the insect outbreak, a heretical objective. To do this, we distributed tons of sugar and sawdust to prevent nitrogen released in litter decomposition from improving the nutrient status of surviving trees (Waring and Pitman 1985). The success of the project demonstrated the value of being ready to test a joint hypothesis when the situation is ripe; and to design experiments to obtain and understand the full realm of possible responses.

Although we could correlate tree vigor with changes in monoterpene composition in growth room experiments (Hyland 1980), we needed a simpler quantitative index to characterize the susceptibility to bark beetle attack of trees in the field. Hundreds of trees were available on which pitch tubes identified the density of beetle attack. Mortality was easy to judge because when attacks are lethal, beetles introduce a fungus that stains the sapwood blue and dries it out. At that time, we knew also that sapwood area was related to leaf area. Allometric relationships established during the IBP allowed us to estimate stem biomass increment from changes in stem diameter (Gholz et al. 1979). These established relationships meant that any forester with a diameter tape and an increment borer could calculate the stemwood biomass growth per unit of leaf area, and thus rank the resistance of individual trees or stands' to bark beetle attack. By providing support to other entomologists, we were able to confirm the generality of the approach by including other tree species attacked by bark beetles (Larsson et al. 1983, Mitchell et al. 1983, Christiansen et al. 1987).

Additional physiological insights and silvicultural options were obtained during an outbreak of defoliating insects when we joined with United States Forest Service entomologists to mount another thinning and fertilization experiment (Mason et al. 1992, Waring et al. 1992, Wickman et al. 1992). The damage done by root pathogens was also shown to be correlated with the structural index to tree vigor (Oren et al. 1985, Waring et al. 1987), but fertilizing with nitrogen to improve stem growth was shown to be ill advised because roots could starve themselves for resources to maintain a healthy biochemical balance in terms of the ratio of phenolics to sugars (Matson and Waring 1984, Entry et al. 1991*a*, 1991*b*).

For their help in building these bridges between physiology and pest control, I owe much to my colleagues in entomology and pathology who invited me to share ideas at a number of their regional and national meetings. It was from these experiences that I met a cadre of people who helped develop some interesting, testable hypotheses. As a result of those discussions, we were ready to install a landscape level experiment when the opportunity arose.

Global change research

Stable isotope analyses

The incorporation of physiological principles into global change research has occurred at a range of scales. Stable isotope analyses and remote sensing are tools that have proven particularly valuable in expanding across time and space scales. In 1985, I participated in a workshop designed to evaluate the possible biological responses at the regional level to a hypothetical "nuclear winter" (Waring et al. 1985). At that meeting, Joe Berry from the Carnegie Institute at Stanford University contributed many insights from his knowledge of photosynthesis and how that process affected the stable isotope composition of plants and the surrounding atmosphere. Through him, I was invited to attend a Gordon Conference on the subject, and thereafter took a year's leave of absence to the Ecosystem Center at Woods Hole, where isotope analyses were part of both aquatic and terrestrial studies.

Although I expressed much interest in the potential use of stable isotope analyses at several symposia, it was difficult to mount a project on a campus without a stable isotope laboratory. I expressed my frustration to my long-time friend Warwick Silvester who ran the stable isotope laboratory at the University of Waikato in New Zealand. As luck would have it, he was interested in a project we had discussed earlier, and if I could come for six weeks, we might complete the test, with a guaranteed 24-h turn around for isotope analysis. Extensive radiata pine plantations and wind breaks, first seen in slides at Professor Stone's lectures at Berkeley, were perfect for demonstrating the effects of branch length on gas exchange and carbon isotope fractionation, and helped explain growth differences in plantations (Waring and Silvester 1994, Walcroft et al. 1996). What seemed like a record accomplishment in cross-disciplinary research, however, was built on more than five years of preparations, 15 years of friendship, and a hypothesis waiting to be tested.

Back in Oregon, we continued to depend on Professor Silvester's laboratory for our stable isotope analyses (Yoder et al. 1994). But when Jeanne Panek, a Ph.D. student, came to Oregon State in 1992 and needed formal training in isotope analyses, we faced a problem. James Ehleringer at the University of Utah solved it by allowing Jeanne to come to his isotope laboratory for a full semester. As a result of his support, she was able to establish that the isotopic composition of foliage and tree rings of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*) closely matches that predicted from a process model (Panek and Waring 1995, Panek and Waring 1997). Plant processes of course also affect the isotopic composition of the Earth's atmosphere and provide a means of identifying changes in the sources and sinks of carbon regionally and globally (Ehleringer and Field 1993).

Remote sensing

Global change programs include a large number of people with experience in remote sensing, but sponsoring agencies like the National Aeronautic and Space Administration (NASA) have made it a policy to invite scientists from a wide range of disciplines to participate in designing and testing instruments. I was fortunate at one NASA workshop to meet Samuel Goward from the University of Maryland. His background in physics and geography attracted students whose research occasionally involved laboratory and field measurements.

With Professor Goward's guidance, technical support from Darrel Williams at Goddard Space Flight Center, and the availability of an ultralight aircraft flown by Rich McCreight, we designed a multi-stage test to determine what biophysical variables a satellite-derived greenness index actually measured. The tests were carried out under controlled laboratory conditions (Yoder and Waring 1994), with ground level measurements (Goward et al. 1994*a*), and from aircraft and satellites (Goward et al. 1994*b*). As a result of these multiple level tests, we recognized that the greenness index was more a measure of photosynthetic capacity than of canopy leaf area, and that background and atmospheric properties could seriously affect interpretation unless taken into consideration (Goward et al. 1994*b*).

Remote sensing scientists, like tree physiologists, are specialized. To gain a better perspective of what a field has to offer, chairing a committee whose charge is to translate concepts from another field to yours provides a quick education. During a stint at NASA headquarters, I served this role for the imaging radar community. In the end, some previously unrecognized opportunities emerged, such as testing whether imaging radar might assess plant water status across landscapes (Waring et al. 1995*a*).

Modeling

To develop models driven from satellite-derived data requires not only a recognition of what can be monitored from space, but also a reconfiguration and simplification of basic model structure. In doing this, as shown in interpreting remote sensing signals, it is desirable to progress upward in steps. Models of canopy processes that operate at hourly time steps for multiple layers must be modified to operate at daily and monthly resolution with much reduced detail. At each step, new approaches may be required to implement and to test the models (Running and Hunt 1993, Waring et al. 1995*b*).

The most integrative contributions to modeling often emerge through comparative studies. John Monteith, a biophysicist, leads my list in showing the merits of this approach in his development of a general canopy energy exchange equation (Monteith 1965) and the concept of radiation-use efficiency (Monteith 1972). More recently, Kelliher et al. (1995) showed from an exhaustive analysis of many studies that the maximum canopy conductance approaches a constant at LAI > 3.0. In carbon balance analyses, Michael Ryan (1991) laid out an approach that calculates annual gross primary production by accounting for all major components. From a dozen comparative studies in temperate forests, Ryan's analysis indicates a nearly constant ratio of net primary production to gross production (Waring et al. 1998). These and other similar synthetic analyses provided the basis for Joe Landsberg at CSIRO in Australia and I to assemble a generalized model of forest productivity (Landsberg and Waring 1997). Nicholas Coops, a CSIRO expert in remote sensing technology, further modified this model to be driven with monthly satellite data across much of southeastern Australia (Coops et al. 1998).

Connections between fields

Although the examples provided in this essay cover a wide range of fields, each situation demonstrated how scientists in different disciplines can work together to gather data, gain insights, reach conclusions, and expand scientific (and practical) opportunities more quickly than if they had simply stayed within their own field. In essence, these are examples of successful bridge building. Bridges are built most quickly when representatives of different disciplines see mutual advantage in collaboration and seek to quickly demonstrate that potential. Usually, however, the process is laborious, because concepts and techniques must be modified and comparative studies conducted before construction can be started at a higher level of integration.

Successful bridge builders are characterized by curiosity and a willingness to take chances, but they are not foolhardy. They have, almost without exception, established credibility in their own field and identified at least one kindred spirit with similar credentials in another. They usually insist on some kind of pilot study that should involve apprentices as well as established scientists. If successful, the younger members of the team may take the lead in further advancements, for which their mentors and teachers should take pride, and learn as well.

Progress in science often comes slowly and all fields languish at times, perhaps awaiting, as the German proverb goes, "new methods, new concepts, and funerals." Managers need to recognize that failure to advance in one field is rarely a sign of incompetence. To keep productive at such times, participation in multi-disciplinary workshops and conferences has special value. Having helped establish a few bridges, I can confirm that it is an exciting venture and that once established, crossing disciplinary bridges is a rewarding experience.

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