RP551

COUPLING STRESS PHYSIOLOGY WITH ECOSYSTEM ANALYSIS

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ABSTRACT

To improve our understanding of how ecosystems operate, identify whether they are under external or self-induced stress, and prescribe appropriate cures, a marriage between stress physiology and ecosystem analysis is advocated. How carbon products are distributed within plants is a sensitive measure of stress; similarly, the quality of detrital carbon reflects the nutritional status of its source and the rate at which it may be processed by heterotrophic organisms. Biochemical indicators such as adeno-phosphate ratios and levels of stored metabolites also may provide insight into the early development of stress. Subtle stress experiments in ecosystems are presented as alternatives to conventional analyses.

INTRODUCTION

Physiologists commonly view stress as part of a process through which the environment induces a defensive response by an organism. Sometimes, stress has been considered the cause and the organism's response, the strain (Cannon 1935, Levitt 1972). Other times, the environment has been designated the stressor and the response by the organism, the stress (Selye 1956, 1975). In all cases, however, the focus has been on living organisms, and has usually been on those not competing with other species.

Most ecologists too have focused upon the responses of living organisms in stressed communities. But unlike physiologists, they have studied mixed populations. In fact, their most common measure of the effects of stress has been the loss of groups of organisms from a community; this has been especially well documented for forests exposed to chronic irradiation (Woodwell 1970).

Only a few ecosystem studies have quantified how stress might affect accumulation or loss of materials independent of changes in the populations of organisms. O'Neill et al. (1977) reported that when soil microbial organisms are subjected to increasing concentrations of heavy metals, their ability to process litter decreases, and additional nutrients are lost by leaching before any population changes are measurable. When such groups of stressed organisms are less able to perform key ecosystem functions, some kind of adaptation will probably result, as illustrated by genetic selection imposed through air pollution upon eastern white pine (Pinus strobus L.) (McLaughlin et al. 1982). But in all cases, ecosystem stress should be defined physiologically.

In this paper I develop the theme that stress physiology is a basis for ecosystem analysis when ecosystem components are linked through a chain of processes coupling autotrophic and heterotrophic organisms. In this coupling, carbon allocation and its chemical bonding with other elements is especially important.

SELF-INDUCED STRESS

Changes in climate or additions of toxic compounds clearly can stress ecosystems. Less apparent, but far more common, is the self-induced stress resulting from two related conditions: (1) increasing maintenance respiration as plant biomass accumulates, and (2) reduced availability of nutrients and sometimes water.

Left undisturbed, forests develop canopies that maximize the interception of solar radiation and uptake of carbon dioxide. Eventually, height growth of trees must slow or cease as net primary production is channeled toward replacing tissues rather than further accumulating biomass. At this time, if not before, limitations in carbohydrate availability force the system to draw down reserves and allocate resources only to essentials. These are symptoms of self-induced stress.

The development of nutrient stress is closely related to how carbon is allocated. As forests age, their demands for nutrients are reduced, but a larger proportion of annual litterfall is woody material. Mineralization of woody material is much slower than that for other forms of detritus; therefore, nutrient release through decomposition is diminished. Plants can internally redistribute critical nutrients, which may further impoverish litter. Eventually, trees are forced to allocate more carbohydrates to roots (Grier et al. 1981) and have even less to utilize in biomass accumulation or in building storage reserves. Because water penetration is reduced as litter accumulates, symptoms of stress other than those associated with nutrient deficiencies also may develop.

Self-induced stress may generally explain why large tree species are eventually replaced by smaller ones that demand fewer nutrients and less light, as is commonly observed in forest-succession studies. Moreover, self-induced stress may partly explain the periodic nature of outbreaks of defoliating insects (Mattson and Addy 1975).

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CARBON ALLOCATION

If proportionally more carbohydrates are allocated to roots, and nutrients and water are limiting, then fewer resources are available for other purposes. Observing the distribution of carbohydrates when in less than optimal supply, stress physiologists generally report that a plant's extremities receive first call for resources because new buds and feeder roots are essential. Fortunately, the growth of various tissues usually is out of phase. Root growth is initiated first in the spring, followed by flower production, then vegetative growth. Often, only after most tissue growth is nearly complete do levels of protective chemicals and carbohydrate reserves accumulate (Mooney and Chu 1974, Mooney 1972). How carbon is allocated within plants may thus indicate ecosystem stress.

Generally, plants allocate carbohydrates to five broad categories: (1) buds and new foliage, (2) feeder roots, (3) storage reserves, (4) protective chemicals, and (5) supportive tissue. Under optimal conditions, a certain proportion of the total resources might be disbursed to each of these. Under stressful conditions, however, certain categories receive less than normal. For example, if storage reserves are low in the fall, diameter growth of roots and stems may be restricted. If the production of foliage ranks relatively high and that of supportive tissue relatively low, then the ratio of the two can measure stress. As an illustration, compare how the ratio changes in 30-year-old Douglas-fir [Pseudotsuga menziesii (Mirb.) Franco] competing for light under a range of canopy densities. Although the trees are all approximately the same height, those growing where canopies are densest produce less than a third the wood per unit leaf area of those growing where competition is less fierce (Fig. 1).

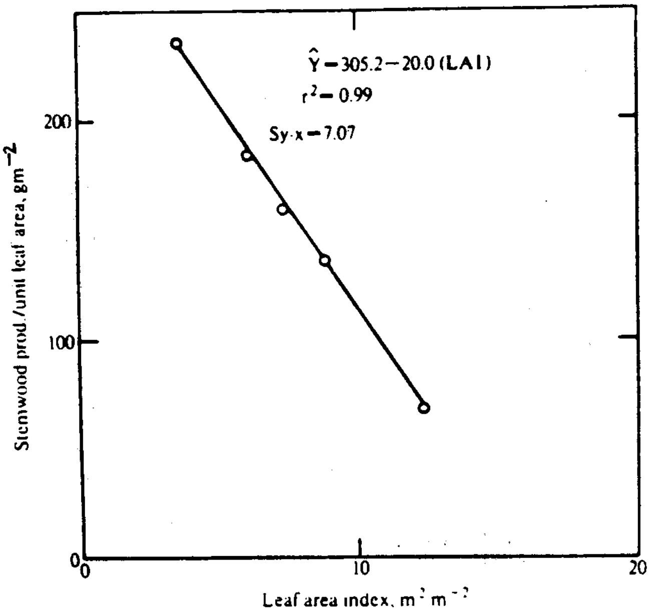

Figure 1.--Net assimilation rate, expressed as stemwood production per unit of leaf area, decreases linearly for 30-year-old Douglas-fir trees as canopy density, expressed as leaf area index, increases (Waring et al. 1981).

DETRITAL CARBON QUALITY

To bridge the physiological gap between primary producers and heterotrophic decomposers--the ecosystem equivalents of anabolism and catabolism--it is essential to evaluate how the quality of detritus changes as plants experience stress.

The simple ratio of carbon to nitrogen in litter and soil has long served as a crude index of the quality of substrate for decomposing organisms and, therefore, the likelihood that minerals might be available for higher plants. More refined studies of decomposition indicate that the kind of carbon is as important as the amount. For example, the decomposition rate in a particular environment often can be predicted on the basis of a substrate's lignin content (Fig. 2).

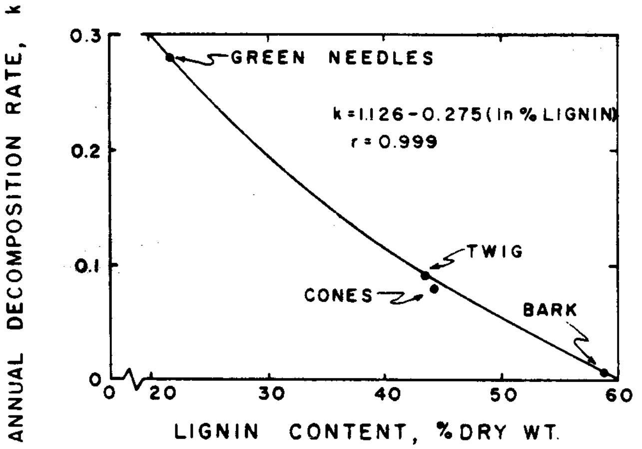

Figure 2.--In comparable environments, the annual decomposition rate is closely related to substrate quality as indicated by lignin content (after Fogel and Cromack 1977).

In addition to lignin, mineral composition and balance are important. Experiments with sustained applications of fertilizers indicate that the composition of leaf litter can be markedly enriched in those added elements (Tamm et al. 1974). Berg and Staaf (1980) took leaf litter from such an experiment and found predictable differences in the rate of decomposition under comparable environments. Thus, the mineral composition of litter, preferably expressed on a unit area basis (Stachurski and Zimka 1975, Smith et al. 1981), indicates both the nutritional stress in plants and the substrate quality for decomposing organisms.

BIOCHEMICAL INDICATORS

Changes in internal biochemistry can be noted long before changes in the population of organisms. White (1980) emphasized that all living cells share through evolution certain common biochemical reactions for regulating the balance between anabolic and catabolic enzyme systems. Under stress, the balance is shifted, and responses may be expressed in a variety of ways. Three broad categories have been recognized:

1. Adeno-phosphate ratios.--Short-term stress can be assessed by measuring adenylate energy charge (E.C.):

$$E.C. = \frac{ATP + 0.5\ ADP}{ATP + ADP + AMP}$$

where

ATP = adenosine triphosphate
ADP = adenosine diphosphate
AMP = adenosine monophosphate

E.C. has been shown to increase in proportion to the growth rate of bacterial cultures (Chapman et al. 1971). This ratio provides a measure of activity, growth, reproductive potential, and stress in both invertebrates and vertebrates and has been used to compare ecosystems (Wiebe and Bancroft 1975).

2. Stored metabolites.--Stresses that induce longer term effects on biota can be measured from changes in pools of endogenous storage materials. Cellular components, stored during periods when the environment is favorable, are catabolized during periods of stress in a definite sequence, with starch-glycogen fastest, triglycerides second, and waxes last. Chronic stress continually draws down starch reserves in trees and has been used to assess their ability to recover from insect defoliation (Webb 1981). Glycogen storage levels in bacteria and animals should serve as an indicator of chronic stress. In the eukaryotes, from yeast to humans, high nutritional status results in triglyceride synthesis and storage; so this may be a useful measure of general health for various organisms in different parts of an ecosystem.

3. Extracellular polysaccharide polymers.--For prokaryotes, the synthesis of extracellular polysaccharide polymers is a sensitive measure of an unfavorable environment, including predation (Williams and Wimpenny 1978). These polymers are recognized by their unique components, such as methylated sugars or uronic acids.

These biochemical indicators could be the harbingers of stress that might later affect more highly evolved forms. Food-chain studies involving the accumulation of toxic chemicals would particularly merit such a biochemical approach.

STRESS EXPERIMENTS

Because ecosystems are composed of a series of interconnected processes involving carbon compounds, stress can be measured anywhere in the series from the living tree, to its detritus, to heterotrophic consumers and decomposers, to soil organic matter and its leachate. Discovering that stress symptoms progress in one direction may indicate early stages of stress, such as that from acid rains or other subtle forms of pollutants. Chronic stress, however, should generate predictable responses throughout an ecosystem but may not permit identification of its initial causes without experimentation.

In the subalpine forests of central Oregon, many stands of lodgepole pine (Pinus contorta Loud.) exhibit signs of chronic stress. Such forests, densely stocked, grow upon relatively infertile soils and are periodically attacked by various insects (see Pitman et al., this volume). Waring and Pitman (manuscript in review) hypothesized that even very old forests might at least briefly recover if stress could be reduced. On this premise, they experimentally decreased stocking levels of lodgepole pine to improve the photosynthetic capabilities of the remaining trees, fertilized with nitrogen to improve their nutritional status, and then monitored selected properties of living plants, their detritus, and soils for 3 years.

The experimental treatment significantly reduced stress symptoms everywhere, as compared to those of untreated stands (Table 1), and in a particular sequence. First, improvements in soil nitrogen were noted, followed by increases in foliar nutrition, quality of leaf litter, and tree net assimilation rate, culminating in improved resistance of the forest to insect attack at epidemic population levels (Pitman et al., this volume; Mitchell et al. 1982).

Table 1.--Changes in carbon and nitrogen properties following thinning and fertilization of a 120-year-old lodgepole pine forest (Waring and Pitman, unpublished).[1]

	Control	Fertilized and thinned
CARBON		
Canopy leaf area index, m^2m^{-2}	4.7	1.0
New foliage in canopy, %	17	31
Net assimilation rate, g wood m^{-2} foliage yr^{-1}	73	120
NITROGEN		
Canopy content, g m^{-2}	4.2	7.3
Inner bark content, %	0.2	0.4
Fine root content, %	0.5	0.7
Fresh leaf litter, g m^{-2}	1.6	2.0
Soil mineralizable nitrogen, ppm	4.4	40.7

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[1] Each treatment was replicated 4 times; values are means from 12 samples. All comparisons differ significantly at the 5% level.

The most informative kinds of stress experiments are subtle. As a good example, Johnson and Edwards (1979) evaluated how changes in the availability of nitrogen and carbon substrate to soil microorganisms might affect heterotrophic activity, as measured by carbon dioxide production, plant uptake of nitrogen, nitrification, and chemical composition of sloughed roots. In their experiments, they included treatments where they (1) girdled trees, (2) added sucrose to the soil, and (3) added ammonium. The results are summarized in Figure 3.

Wherever the carbon substrate for soil heterotrophs was increased, additional nitrogen was mineralized and more carbon dioxide generated. Where an additional source of nitrogen also was provided, as from the death of roots in the girdling treatment or from added ammonium, more carbon substrate also became available. The result was increased nitrification and uptake by trees.

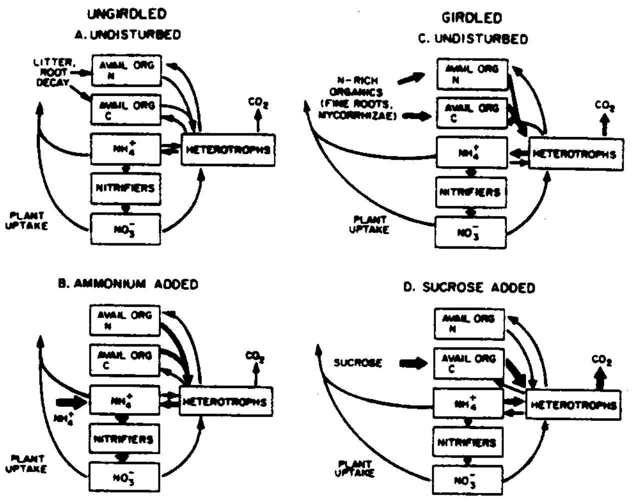

Figure 3.--Ecosystem response to changes in the availability of carbon and nitrogen to microbial organisms. Treatments that increase carbon supply (D) inhibit nitrifiers and plant uptake while favoring heterotrophs. When the nitrogen supply is enhanced alone (B) or in concert with available carbon (C), nitrification and uptake are both increased. The relative thickness of arrows indicates the magnitude of fluxes (Johnson and Edwards 1979).

Neither the Waring and Pitman study nor that of Johnson and Edwards (1979) was comprehensive in evaluating all ecosystem components; no attempts to account for total allocation of nitrogen or carbon were made. Yet both studies offer evidence that subtle stress experiments can provide insight into the functional efficiency of carbon uptake, allocation, and utilization.

Stress physiology may, I believe, offer a better framework for gaining understanding of how ecosystems operate than conventional approaches. A balanced interest in autotrophs and heterotrophs and in the substrate quality of living and dead tissue provides a marriage between stress physiology and experimental ecosystem studies that promises to be fruitful.

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