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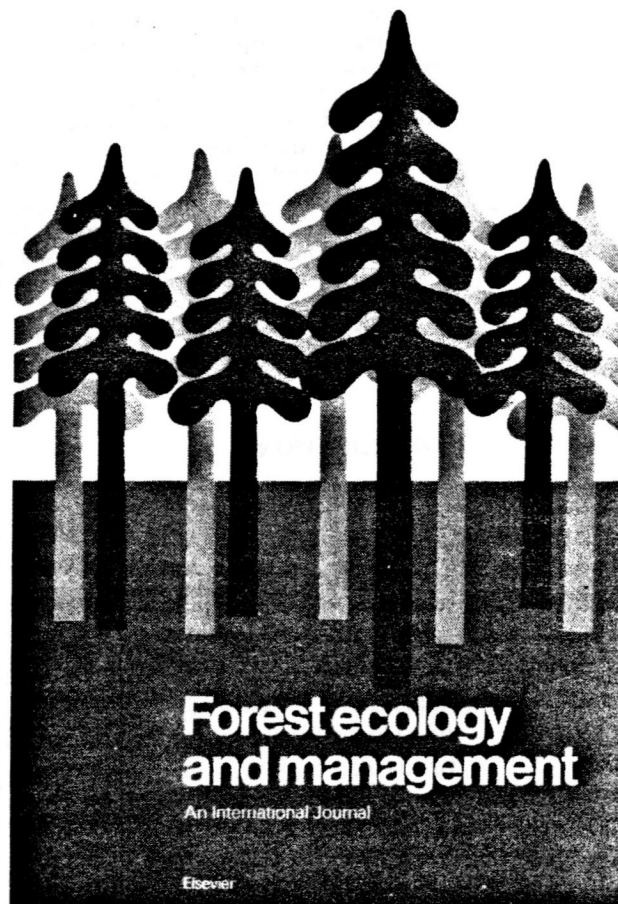
**IMBALANCED FOREST ECOSYSTEMS: ASSESSMENTS AND
CONSEQUENCES**

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(Accepted 26 February 1985)

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ABSTRACT

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Few ecosystems can maintain an ideal balance of available resources for primary producers, decomposing organisms, and consumers. When nutrition is optimal for plants, their tissue may be toxic for many consumers and their detritus nutritionally imbalanced for decomposers. Even conditions favoring high rates of primary production soon lead to limitation in light and possibly other resources. Because of the integrated nature of ecosystems, stress induced in one part permeates the entire system. With chronic stress induced by climatic change or air pollution, we might expect reductions in canopy leaf area, decomposition rates, and root mineral uptake, and increases in herbivory, pathological activity, and leaching of material into or through the rooting zone. Each of the six responses can be simply assessed. As a general index of stress to forest ecosystems, we may monitor changes in the ability of foliage to produce wood. Below a particular level of production, trees become susceptible to a variety of insects and diseases. Through an experimental approach, we can identify the relative importance of constraining factors and predict the consequences of management options.

INTRODUCTION

Many studies of the last few decades have monitored the environment and illustrated some of the complex ways in which chemicals, light, and water interact within biological systems. We have gained considerable understanding of major ecological relationships, and from this knowledge have begun to establish new techniques of assessment. This paper reviews some of these techniques and discusses their effectiveness and application in stress analysis of forest ecosystems. Initial emphasis is upon finding general indices of stress. Where stress is documented, additional indices can indicate the probable cause. An experimental approach is then advocated to confirm the diagnosis and offer insights as to how imbalances in available resources might be corrected.

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As we all recognize, forest ecosystems are buffered against minor fluctuations in weather and can withstand temporary reduction in the biomass of key components such as the photosynthetic canopy, microbial populations in the litter, and major consumers. Behind the apparent structural stability of a 100-year-old forest, however, we may find significant changes occurring. General reductions in storage of carbohydrates, related to the cost of maintaining respiration, may make the forest susceptible to attack by insects or pathogens. Atmospheric enrichment with nitrogen, sulfur, and heavy metals may initially improve but later reduce the availability of critical minerals (O'Neill et al., 1977; Hari et al., 1984).

The response of ecosystems to subtle imbalances is a series of interconnected adjustments. Knowledge of the extent of these adjustments and their consequences is the key to selecting integrative indices for identifying the causes of and cures for various stresses. The following sections will define a host of stress indices, illustrate their utility, and advocate an experimental approach for evaluating the relative importance of various constraints upon primary production and ecosystem "health" in general.

STRESS INDICES

If we are looking for connections among the biological and physical-chemical processes, it is helpful to view ecosystems in a conceptual frame-

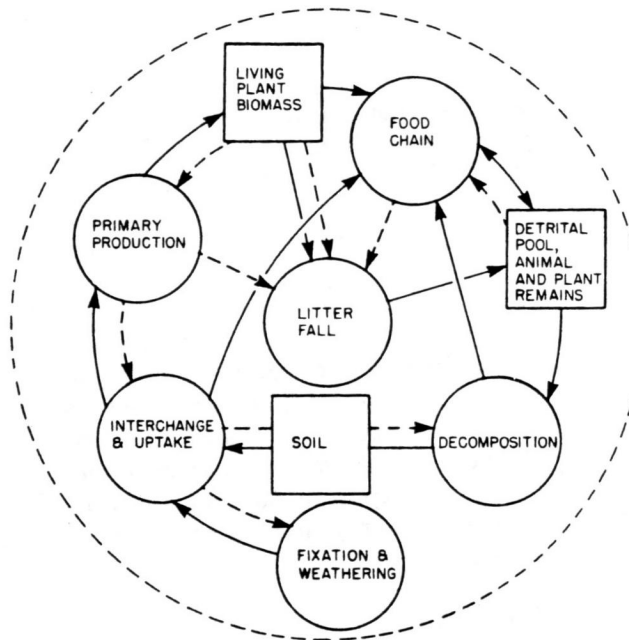


Fig. 1. Major sets of processes active in terrestrial ecosystems, represented by circles, are connected to one another, directly or indirectly. Major storage sites for carbon compounds, water, and minerals are represented by squares. (After Overton, 1972.)

TABLE 1

Forest ecosystem stress indicators

Indication	Examples
Canopy limitation	Maximum leaf-area index Duration of leaf display
Production limitation	Diameter growth and cell division Growth efficiency per unit leaf area
Susceptibility to insect and disease attack	Starch content of twigs and large roots Tannin and terpene content of tissues Growth efficiency per unit leaf area
Moisture limitations	Pre-dawn water stress Noon leaf turgor Sapwood relative water content Stomatal closure
Nutrient limitations	Foliar nutrient content Foliar nutrient ratios Nutrient retranslocations Mineralization indices Excised-root uptake
Physical stress	Sapwood/diameter index Bole taper Symmetry of wood growth Flag-edge tatter

work similar to that illustrated in Fig. 1. The influence of one set of processes, such as that involved in primary production, permeates all routes to affect all other sets of identified processes. The buffering of terrestrial ecosystems depends, for the most part, upon sites where carbon products, water, and minerals may be temporarily stored: the living biomass, the detrital pool, and the soil.

By searching for chemical or structural adjustments that occur over an entire season or year, we may identify stress that can become chronic. Also, by extending our search from short-term to seasonal or annual indices, we should be able to find those that are more widely and more economically applicable. Six index classes of ecosystem stress are shown in Table 1. Many of these are derived from measurements on relatively large plants that have continual exposure to the atmosphere and soil and that represent the source of energy and nutrition for most other forms of life active in the system.

The canopy

One of the most general of stress indices is the amount of canopy a forest develops, and the seasonal duration of leaf display. Whether we look at an

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ecosystem from the ground or from a satellite, the canopy is an indicator of productive capacity — the dense canopy of a redwood forest easily contrasting with the sparse coverage of a juniper woodland. Even within one forest type, variation is apparent. Above 1 m² of deciduous hardwood forest there may be from 3 to 6 m² of leaf surface (counting only one surface), or above 1 m² of spruce forest there may be from 8 to 12 m² of projected needle surface (about 40% of total needle surface). The problem is how to measure this leaf-area index accurately without direct sampling.

Many indirect indicators of canopy density relate to the intercepting properties of leaves. Multispectral scanners in aircraft or satellites above the forest are one possibility for indirect measurement, although the effects of air pollution, insect activity, and drought may confound interpretation (Puritch, 1981). Microwave transmission (Stuzman et al., 1979), side-looking radar (Langley, 1976), or laser beams (Arp and Burns, 1979) are active signals that may provide better resolution, particularly in dense canopies. On the other hand, reflective properties of canopies in the red and infrared portions of the spectrum have already proven useful in estimating canopy leaf area (Spanner et al., 1984), chlorophyll concentration (Goetz et al., 1983), and possibly seasonal photosynthesis (Tucker, 1985).

From the ground, canopy leaf area can be estimated from correlations with stem diameter (Whittaker and Woodwell, 1968). This technique assumes that trees have proportionally more canopy as they grow larger; but if stressed, a canopy can be reduced while the diameter of trees does not change.

The most accurate estimate of canopy leaf area, for an entire forest or for individual trees, requires an estimate of sapwood cross-sectional area (Waring et al., 1982). Estimates of sapwood are made by determining tree diameter and extracting a small wood core to find the thickness of sapwood.

Ground sampling techniques have shown ten-fold differences in the leaf area index (LAI) of mature coniferous forests along steep environmental gradients (Grier and Running, 1977; Gholz, 1982). In deciduous forests, where the canopy is less variable, the duration of leaf display during the year becomes more important. Relative changes in the canopy can be estimated by periodically sampling the development of foliage or by rephotographing the canopy from the ground or air.

Production

Within broad regions, the maximum canopy that coniferous forests develop is rather closely associated with the dry-matter production of stem and branchwood (Fig. 2). In hardwood forests, the product of leaf area index and number of months that leaves are displayed is a fair index to production (Fig. 3); thus a long-term change in climate or amount of pollution in the atmosphere should result in a change in the maximum leaf area and the duration of display.

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relate to the intercepting aircraft or satellites above the forest, although the effects of canopy confound interpretation (Burns et al., 1979), side-looking radar (Burns, 1979) are active especially in dense canopies. On the other hand, the use of the red and infrared is useful in estimating canopy concentration (Goetz et al., 1985).

estimated from correlations (Schroeder, 1968). This technique is only as good as they grow larger; but the diameter of trees does not

for an entire forest or for cross-sectional area (Waring, 1979). Determining tree diameter is a measure of sapwood.

old differences in the leaf area index (L) along steep environmental gradients (Schroeder, 1982). In deciduous forests, the leaf display during the growing season in the canopy can be estimated by the amount of foliage or by

that coniferous forests produce more stemwood per unit leaf area than deciduous forests. The product of leaf area index (L) and the number of months of the growing season (S) is a fair index to estimate the amount of foliage in the maximum leaf

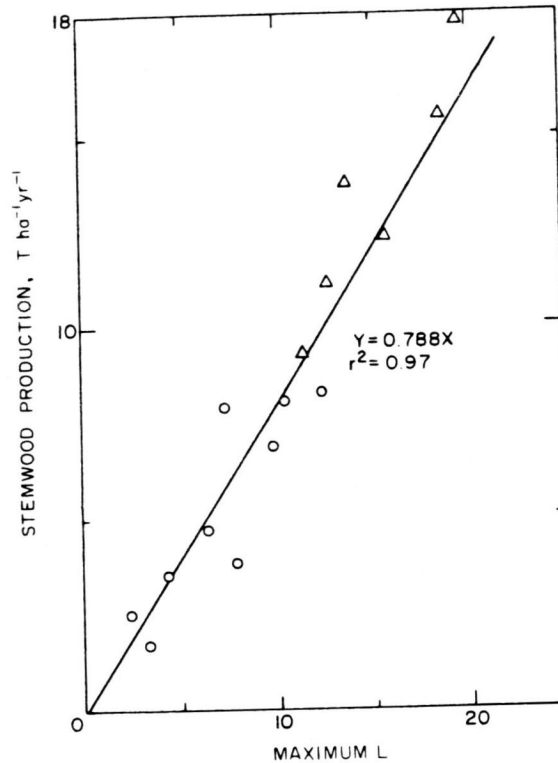


Fig. 2. Across a steep climatic gradient in the mountainous region of eastern Washington, annual production in mixed coniferous forests increases directly with maximum leaf area index (L) (Schroeder et al., 1982).

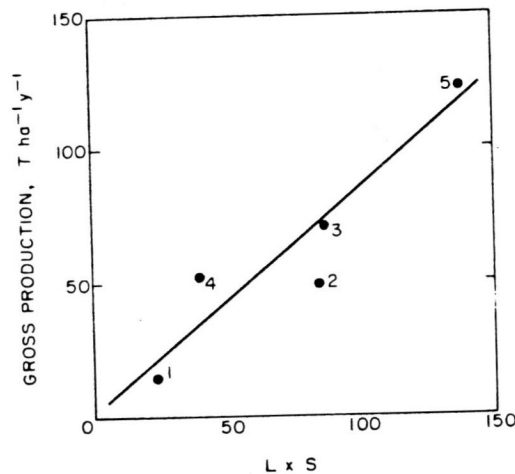


Fig. 3. Gross primary production in temperate or tropical hardwood forests is related to the product of the leaf-area index of the canopy (L) and the number of months of the growing season (S). (1) *Fagus* forest in Denmark; (2) *Castanopsis* forest in Japan; (3) broad-leaf forest in Japan; (4) tropical humid forests of the Ivory Coast in Africa; (5) tropical forests of southern Thailand. (From Kira and Shidei, 1967.)

Even without changing its leaf area, a tree may become more efficient in producing dry matter, as, for example, when competing trees are removed. Conversely, a tree suddenly shaded by another's canopy may become less efficient. As the amount of stem or branchwood can be estimated from correlation with diameter (Whittaker and Woodwell, 1968), changes in diameter over a known period can be converted into biomass increment.

For estimates of recent growth, growth rings can be measured on wood cores taken from trees. In the tropics, where many trees do not produce distinct annual rings – or wherever seasonal responses to changes in critical environmental variables are of interest – cambium activity may be disturbed by inserting a small pin into the tree, which thereafter produces distinct kinds of wood cells that permit precise identification of wood production over short or long periods (Gregory, 1971; Emmingham, 1977).

Wood production per unit of leaf area is a measure of growth efficiency applicable to all trees. This index can be calculated on individual trees or can be averaged for a stand. Tree-diameter measurements and wood cores are all that are required if relationships of diameter and stemwood biomass and of

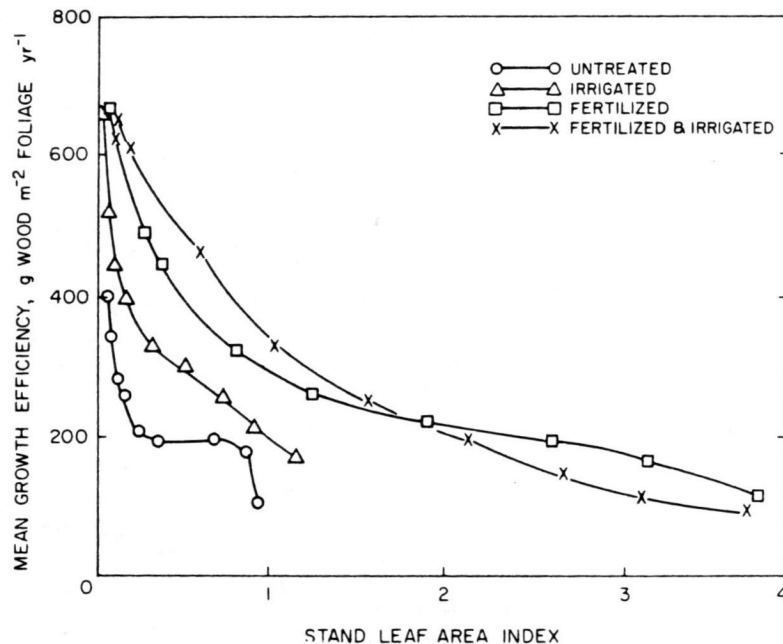
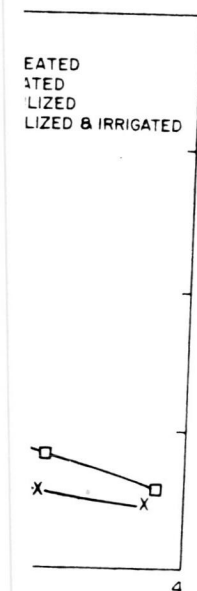


Fig. 4. Saplings of Scots pine grown over a decade under differing nutrient and water regimes initially showed large differences in growth efficiency among treatments. As the stands approached their maximum leaf area indices at 10 years, however, growth efficiency became comparable. The leaf area indices differed more than three-fold and directly relate to the present differences in annual biomass increment per hectare. (Unpublished data analyzed by Waring, Axelsson, Aronsson, and Linder. Experiment described by Aronsson et al., 1977.)

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sapwood cross-sectional area and leaf area are known (Waring et al., 1980b; Waring, 1983).

As young seedlings grow into saplings, and as the canopy of a forest begins to close, the growth efficiency index decreases abruptly. Fig. 4 shows the relationship between growth efficiency and the stand leaf area index of young Scots pine as a canopy closes over a decade. Efficiency is reduced four- to six-fold, depending upon whether the stand is untreated, irrigated continually during the growing season, fertilized annually, or fertilized and irrigated (Aronsson et al., 1977).

Differences among treatments in terms of growth efficiency are best compared at similar indices of canopy leaf area. To compare the untreated stand with the others in Fig. 4, we must have a reference of about $1 \text{ m}^2 \text{ m}^{-2}$ LAI, the value near the maximum obtained by the control. Trees in standards receiving the other treatments obtained 1.0 LAI much earlier than in control stands, but at that value growth efficiency was from 100% to more than 250% higher than that of untreated Scots pine. After a decade, the stands showed relatively little difference in production per unit of leaf area. Fertilizing, however, increased the maximum LAI more than three-fold.

As a measure of competition (Waring et al., 1981) or as an aid in defining the relative importance of various stresses, the growth efficiency index is a valuable tool (Waring, 1983), even serving as a basis for assessing the risk of insect attack in certain kinds of forests.

Secondary compounds

Until recently, evaluating the susceptibility of plants to diseases or insect attack required inoculation of plants with organisms so that the responses could be observed (Tani et al., 1975; Raffa and Berryman, 1982). This approach has little utility in evaluating general changes in the susceptibility of plants to the insects and diseases that periodically ravish forest vegetation. In the extensive pine forests of western North America, the growth efficiency index appears to be a means of rating the susceptibility of individual trees and stands to bark beetle attack and possibly also to attack by various defoliating insects (Pitman et al., 1982; Larsson et al., 1983; Mitchell et al., 1983). On both ponderosa and lodgepole pine, the risk rating increases exponentially when production falls below about 100 g m^2 foliage.

Associated with a decrease in growth efficiency is reduced production of terpenes and of the resins that encase insects or pathogens (McLaughlin and Shriner, 1980; Raffa and Berryman, 1983; Waring and Pitman, 1985). The reasons are varied, but certainly the lack of sufficient carbohydrates leads to reduced terpene production (Croteau et al., 1972).

In conjunction with the growth efficiency index, analysis of starch reserves in the twigs of conifers is proving to be an excellent indicator of the defoliation a tree can withstand and still produce new foliage (Webb, 1981). This indicator seems reasonable because of the high requirements for

carbohydrates during bud expansion and because stored carbohydrates throughout the plant are used, along with current photosynthate, to produce protective compounds when a tree is attacked. The high concentrations of tannins and other compounds in the tissue of many forest trees make them unpalatable or toxic to a wide variety of organisms (Feeny, 1970; Rhoades and Cates, 1976; Fox, 1981). The biological actions of tannins may include forming complexes with plant proteins, reducing the digestibility of tissues to insect or vertebrate herbivores, or forming complexes with digestive enzymes. Recently developed is an efficient test of the complexing capacity of tannins — a test which may be performed even on individual leaves. Blood hemoglobin precipitation is the basis for assaying the effectiveness of tannins and related compounds (Bate-Smith, 1973; Schultz et al., 1981).

Water relations

Any hydrologic constraint upon forest production must ultimately be linked to effects upon plant water relations. Large, well-rooted trees exhibit less water-related stress than younger plants, which may succumb during a short drought (Waring and Cleary, 1967).

With the introduction of the pressure-chamber technique (Scholander et al., 1965) for estimating plant water stress, cellular osmotic characteristics, and cell turgor, it has become relatively simple to evaluate how much soil drought affects water uptake, how seasonal osmotic adjustments accommodate chronic periods of drought or frost, and when cell turgor is reduced sufficiently to force stomatal closure and halt growth above ground.

Well-rooted trees can remove as much as 75% of the available water in the soil before any reduction in water uptake is noted (Whitehead and Jarvis, 1981). In extracting the remaining available water, however, trees undergo progressively higher stress (Sucoff, 1972) that can be quantified by sampling foliage before dawn, when transpiration is minimal. The water stress, or potential, at that time directly affects the extent stomata may open during the day (Fig. 5). If we measure water stress at a time of year when stress is most likely, we find a range of values (Waring and Cleary, 1967). A separation of environments is best obtained by measuring just before the commencement of rainy weather. In Fig. 6, distinctly different patterns are recorded for 2-m tall Douglas-fir trees growing in forests dominated by oak, pine, and spruce.

In regions with the cold soils and long spring days characteristic of the boreal forest zone, water may be abundant in the soil, but uptake may progressively lag behind transpiration, forcing trees to withdraw water from conducting tissue of branches and stems (Fig. 7). Eventually, so many water columns may be broken that the gradient for moving water from the roots to the foliage is too steep, and stomata are forced to close (Waring and Running, 1978). To evaluate the importance of this kind of stress, small

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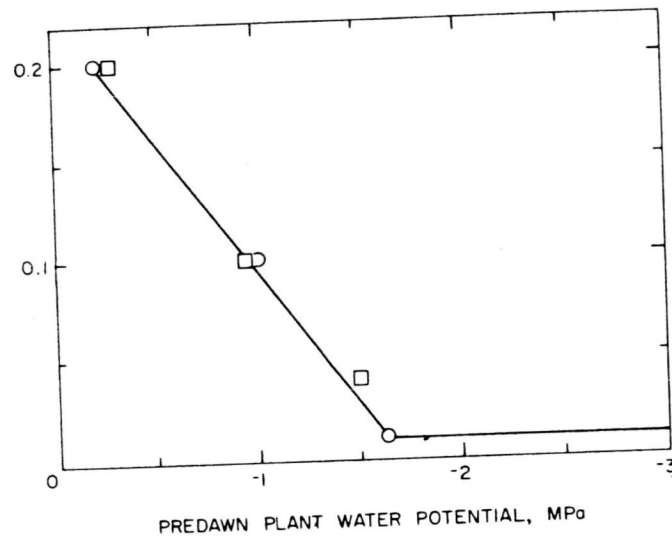


Fig. 5. Predawn plant water potential controls the maximum opening of stomata in hard-woods such as *Liriodendron tulipifera* (□) and conifers such as *Pseudotsuga menziesii* (○). When the stomata remain closed during the day, bulk turgor in the leaf approaches zero. (After Waring et al., 1980a.)

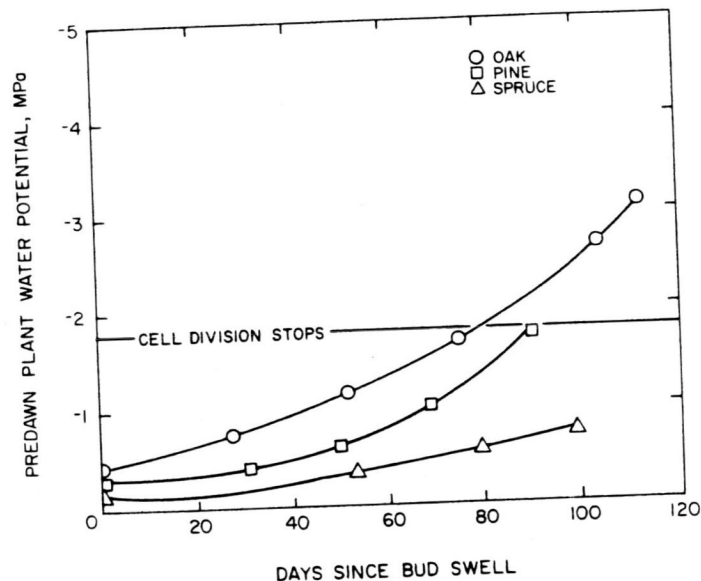


Fig. 6. In regions commonly having long drought, predawn measures of plant water stress are useful for characterizing the extent of drought and the effects on growth of the cambium or on stomatal control (see Fig. 5). Here data are contrasted for 2-m tall Douglas-fir growing in forests dominated by oaks, pine, and spruce. (After Waring et al., 1972.)

cores of sapwood must be sampled after periods of clear weather. Low relative water content is an indication of problems with water uptake. Further measurements and possibly experiments may be required to identify the cause, as even infection by root rot can result in reduced sapwood water content.

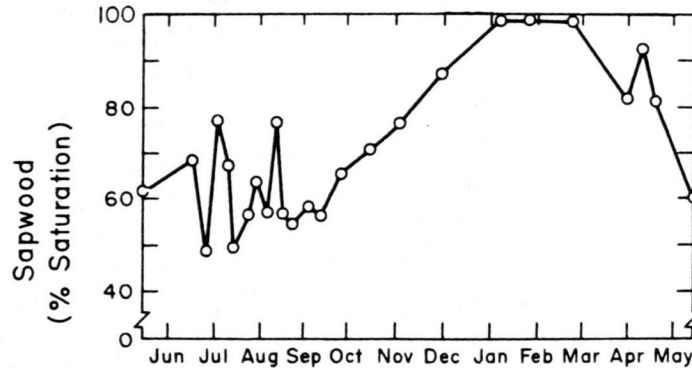


Fig. 7. Monthly recording of sapwood water in 500-year-old Douglas-fir growing in the Cascade Mountains of western Oregon indicates that nearly half of all free water in the wood is removed during the extended summer drought. Partial recharge occurs after storms, but full recharge is delayed until winter, when the evaporative demand remains low for more than a month. (After Waring and Running, 1978.)

Stomata may be forced to close, regardless of favorable water status of a tree, if air humidity is much above 2 kPa vapor pressure gradient (Whitehead and Jarvis, 1981), if roots are flooded and unable to obtain sufficient oxygen (Hinckley et al., 1981), or if leaf temperatures drop much below freezing (Drew et al., 1972). If these circumstances are common, it may be desirable to confirm the water status by monitoring stomatal behavior on intact plants (Running, 1976) or by sampling excised foliage quickly (Reed and Waring, 1974).

It should be noted that reduced tree growth can be associated with partial utilization of water in the rooting zone before plant water relations are affected. Growth reductions reflect, in these cases, an increasing allocation of photosynthate to the roots and not a reduction in photosynthesis due to water stress (Linder and Axelsson, 1982; Waring, 1983).

Mechanical pressures

In many regions, high winds, heavy snow, or rime ice limit the kind of vegetation and its growth rate. Where forests are to be reestablished, as in the Scottish highlands, it may be desirable to assess the impact of high winds before determining the kind of trees to plant and whether growth rates will sufficiently reward the effort of establishing new plantations. For such purposes, flags of standardized material, dimension, and height can be

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positioned on the sites to be evaluated. The flags should swivel freely. After exposure for months or even a year, the amount of fabric worn away is recorded, and the amount of tatter is exponentially related to wind speed (Thomas, 1959). Maps may then be constructed, rating various sites as to harshness. In areas where trees are then planted, the tatter rate can be linearly related to observed reductions in height growth. In Great Britain, for example, the height growth of lodgepole pine planted on exposed sites can be predicted from an equation developed by Lines and Howell (1963):

$$\text{Annual height growth (cm)} = 23.8 - 1.4 (\text{cm}^2 \text{ tatter per day})$$

Where forests are well established, high winds, often combined with snow and ice, may lower production, most notably by reducing the amount of canopy. The loss of canopy can be assessed by estimating the amount of green foliage attached to twigs that fall into litter traps; however, that is a laborious technique, and an index called the "sapwood/diameter ratio" may be more practical. From destructive analyses of normal trees, regressions between diameter at breast height and mean foliage area can be developed. The amount of foliage predicted from diameter measurements can then be compared with that estimated from samples of the sapwood. If wind or snow breakage has occurred, the ratio of leaf area estimated from sapwood to that estimated from diameter would be significantly below 1.0. In a study of a 110-year-old western hemlock forest near the Pacific Coast in Oregon, Grier (1976) reported that trees supported only about 70% of the crown expected for their diameter. The losses to wind breakage were confirmed by litterfall collections.

Bole taper is another index of the effects of heavy snow loads on canopies, even where breakage of limbs is not apparent. Additional load on the canopy means that proportionally more wood must be laid down toward the base of the stem. The wood physics explaining this phenomenon are described in general equations by Petty and Worrell (1981). Taper may be easily measured in the lower bole with conventional forest-survey instruments.

When mechanical stress comes consistently from one direction, trees develop asymmetrical forms as counterbalance. If only the base of a tree is asymmetrical, snow or soil creep are likely operating. The extent of these deformations might be quantified to serve as an index.

Nutrition

From extensive physiological experiments on coniferous and hardwood trees, it is increasingly apparent that a balanced nutrient supply is required for optimum growth (Ingestad, 1971, 1979, 1982). Although growth may continue when elements are not in balance, plants must expend more resources in building roots or in translocating critical nutrients. This increased metabolic expenditure may reduce the competitive ability of a tree

and make it susceptible to certain pathogens (Lambert and Turner, 1977). The balance is easily disturbed. Table 2 compares amounts of nitrogen, phosphorus, and sulfur in foliage of Douglas-fir growing in pure stands and in stands with nitrogen-fixing red alder. If we assume that the optimal ratio for N:P:S is 100:20:10, then doubling the amount of nitrogen in the foliage reduces P by two-thirds and alters the ratio to 100:5:5.

TABLE 2

Indices of nutrient balance of 20-year-old Douglas-fir growing in pure stands and in stands with red alder (Reid, 1983)

Index	Pure Douglas-fir	Douglas-fir with alder
N (g m^{-2} foliage)	3.0	6.0*
P (g m^{-2} foliage)	1.0	0.3*
S (g m^{-2} foliage)	0.3	0.3
N:P:S ratio in foliage	100:35:11	100:5*:5*
N:P:S ratio in litter	100:14:17	100:8*:9*
Fraction transferred before leaf abscission (N, P, S)	0.5, 0.4, 0.3	0.6, 0.3, 0.4

*Values differ at $P \leq 0.05$.

A change in the balance of nutrients may affect the amount that can be translocated before leaf abscission. Because foliage carbohydrates may be depleted before abscission and because they may represent more than 30% of the weight, it is desirable to express values in terms of nutrient mass per leaf (Fife and Nambiar, 1984) or leaf area (Stachurski and Zimka, 1975; Smith et al., 1981). In the analysis shown in Table 2, the relative amount of nutrients translocated before leaf abscission partly reflects the degree of imbalance. The litterfall in the alder-conifer stand was enriched in nitrogen but impoverished in phosphorus and sulfur. In bioassay experiments, Douglas-fir seedlings grown on soils from the mixed forest responded to additions of impoverished elements (Binkley et al., 1982), but Douglas-fir in soils from the pure stand responded initially only to additions of nitrogen.

For the most sensitive analysis, foliage or other tissue should be collected at a time when demand is highest (Waring and Youngberg, 1972; Fife and Nambiar, 1984). In the later part of the growing season, nutrients may continue to accumulate or begin to be translocated (Fife and Nambiar, 1984). Deficiencies in some nutrients such as phosphorus or boron affect roots before symptoms appear in foliage. The uptake rate of various elements by excised roots placed in nutrient solutions is an index inversely related to the degree of deficiency (Dighton and Harrison, 1983). Seasonal differences in uptake reflect differences in growth activity (Langlois and Fortin, 1984).

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Nutrient availability

In addition to the mineral composition of detritus, a valuable index to the decay rate is the lignin fraction. Lignin is the component most resistant to decay and is eventually important in the development of soil organic matter (DeHann, 1977). Tree tissues contain varying fractions of lignin; for example, green needles of Douglas-fir may contain 25%, bark nearly 60%. the decay rates of these tissues vary more than four-fold in a predictable manner (Fig. 8). Information on nitrogen and lignin composition of detritus may give an index with wider application than information on one or the other alone (Melillo et al., 1982).

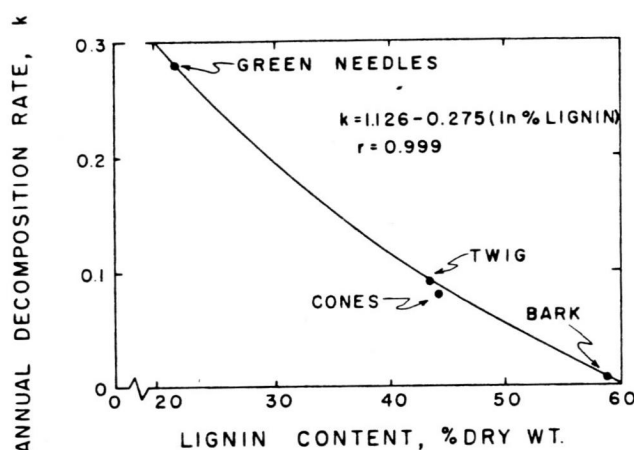


Fig. 8. In comparable environments, the annual decomposition rate is closely related to substrate quality as indicated by lignin content. (After Fogel and Cromack, 1977.)

An alternative to the indirect indices is to follow the actual rate of decomposition and mineral release by detritus over time by placing known amounts of litter into nylon bags, then burying the bags in the forest floor or soil (Fogel and Cromack, 1977). Both decay rates and the differential mineralization rates of various minerals can be derived in this way (Staaf and Berg, 1982). Elements such as calcium, which microorganisms require only in exceedingly small amounts, are quickly released. Elements such as nitrogen, phosphorus, and sulfur are more likely to accumulate initially in microbial biomass and to be released only after considerable detrital weight loss (Fig. 9).

The source of minerals is not entirely decomposing leaf litter or small twigs. Large woody debris may also be a long-term source. As estimates of log decay have been found to correlate with changes in wood density, decay rates may be predicted from chemical and physical analysis of large woody debris (Lambert et al., 1980).

growing in pure stands and in stands

Douglas-fir with alder

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8*:9*

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nglois and Fortin, 1984).

The amount of mineral nutrients available to roots is dependent upon characteristics of the soil and atmospheric deposits, not upon the decay of detritus alone. Although a fair estimate of cation availability may sometimes be gained by soil analyses of exchangeable bases, there are problems in estimating the availability of nitrogen and phosphorus. Mycorrhizal fungi and other microorganisms around tree roots aid mineral extraction when minerals are most available (Bowen, 1982), confounding results. Tension lysimeters that collect samples of water seeping through the soil also may inaccurately represent availability, unless linked to sophisticated hydrologic and physiologic uptake models.

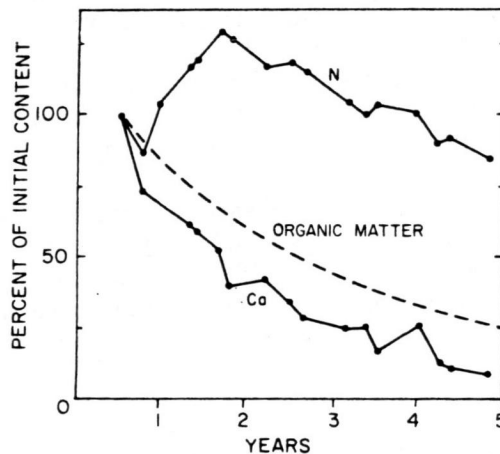


Fig. 9. Mineral content of Scots pine needles changes in the litter over a 5-year period. The needles accumulate minerals such as N, while others such as Ca are quickly mineralized and released. (Staaf and Berg, 1983.)

A promising technique for determining nutrient availability is to package exchange resins in nylon bags and bury these at various places in the root zone for various periods of time (Smith, 1979; Binkley and Matson, 1983). Upon recovery, the ion flux to the resins can be determined and can serve as a comparative index of mineral availability. Initial results are promising (Cromack et al., 1985). Another method is to collect soils and incubate them under aerobic or anaerobic conditions. After incubation, the amount of nitrogen mineralized is an index to availability of this element (Geist, 1977; Powers, 1980).

A STRESS ANALYSIS

Dr. Gary Pitman and I performed a stress analysis on stands of 120-year-old lodgepole pine to evaluate experimentally the relative importance of water, nutrients, and light in improving tree resistance to the attack of mountain pine bark beetle (*Dendroctonus ponderosae*) (Waring and Pitman, 1985).

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We made specific analyses of nitrogen of the inner bark, roots, and foliage. Wherever we looked in the soils, litter, and trees, the initial levels of nitrogen were low (Table 3). Likewise the growth efficiency index was below 100, indicating susceptibility to insect attack. Water relation measurements, even after more than 1 month without rain, suggested no limitation of water to roots, although sapwood reserves were depleted. Conventional wisdom suggested that thinning the forest would provide more water, but thinning experiments showed no difference. Opening the forest canopy allowed grass production to increase, but there was no notable water stress.

Table 3 contrasts nutrients after the most extreme treatment, removal of 80% of the canopy and fertilization with 420 kg N (urea) ha⁻¹, with the situation in untreated stands. Fertilization without thinning resulted in similar changes in nitrogen response, but, because light limited efficient photosynthesis, the production of stemwood and protective chemicals remained below the critical threshold, and many trees were attacked and killed by beetles.

Thinning and fertilization stimulated growth and the ability of trees to produce resin, so that within 2 years most trees were no longer susceptible to attack (Pitman et al., 1982; Waring and Pitman, 1985). We also noted during the experiment that after substantial beetle-induced mortality in the untreated stands surviving trees began to improve significantly. After 4 years,

TABLE 3

Changes in carbon, nitrogen, and water indices after thinning and fertilization of a 120-year-old lodgepole pine forest^a

Index	Untreated	Fertilized and thinned
Carbon		
Canopy leaf-area index (m ² m ⁻²)	4.7 *	1.0
Growth efficiency (g wood m ⁻² foliage y ⁻¹)	73 *	120
Nitrogen		
Canopy foliage (g m ⁻²)	4.2 *	7.3
Fresh leaf litter (g m ⁻²)	1.6 *	2.0
Fraction N retranslocated	0.62 *	0.72
Soil mineralizable N (ppm)	4.2 *	40.7
Water		
Predawn tree water potential in August (MPa)	-0.3	-0.3
Noon tree water potential in August (MPa)	-1.5	-1.6
Sapwood relative water content in September (%)	54	53

^aEach treatment was replicated four times; values are means from twelve samples. Indices differing statistically at the 5% level of significance are identified with an asterisk. (From Waring and Pitman, 1985.)

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most trees that were still living were resistant to further attack. The beetles themselves had performed a less uniform kind of thinning and fertilization.

The stress analysis performed on this century-old forest showed from the start that the trees were under stress and suggested that nitrogen and light were limiting but that water resources were probably adequate. The experimental results were interpretable because the response indices were sensitive to critical processes linking primary production, decomposition, and nutrient and water availability throughout the ecosystem. The approach should have wide application because these processes operate in all forest ecosystems.

SUMMARY

Stress analysis can be performed upon any kind of terrestrial ecosystem. For signs of change, the monitoring of maximum canopy leaf area and its duration of display is recommended. An increase in leaf area suggests an improving environment; a reduction in maximum leaf area is a harbinger of stress. To evaluate the probable cause, key stress indices can be measured periodically throughout the system. To confirm a diagnosis of stress, experiments may modify stand structure, chemistry, and water relations. Selected stress indices can then be of value in following subsequent changes as they permeate the system. The relative importance of various factors or success of various ameliorative treatments can best be judged at equivalent and moderately low indices of stand leaf area.

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