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# Precursors of Change in Terrestrial Ecosystems

*Remote sensing offers new ways to estimate basic ecological parameters that signal change in terrestrial systems*

R. H. Waring, J. D. Aber, J. M. Melillo, and B. Moore III

Satellite remote sensing has proved useful in assessing changes in the extent, density, and composition of vegetation (Botkin et al. 1984). With recent improvement in spectral resolution (Ferns et al. 1984, Goetz et al. 1985), remote sensing from satellites may be capable of identifying on regional or continental scales those ecosystems subject to change. At these scales, general ecosystem characteristics such as net photosynthesis and transpiration, patterns of carbon allocation, plant maintenance respiration, and turnover of organic matter may serve as precursors of change.

It may seem foolhardy to select characteristics of ecosystems that can be so difficult to quantify. But these characteristics represent integrative measures of important processes common to all terrestrial systems supporting vegetative cover. Moreover, sensing a change in the rates of such processes may provide insights even without full quantification of the processes.

At present, no satellite-borne sen-

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## Satellite measurements made between the canopy and the ground can give clues to processes operating belowground

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sor can directly assess ecosystem processes operating belowground. Measurements must be made between the top of vegetation and the ground surface. Fortunately, the canopy is sensitive to changes in the availability of belowground resources (Coley et al. 1985, Waring 1983). In addition, the canopy supplies much of the organic material that falls to the ground and eventually decomposes. It is also the major interface for exchanging carbon dioxide, water, and aerosols with the atmosphere. For all these reasons, looking for subtle changes in canopy extent, activity, temperature, and chemistry should prove useful.

How ecologists might use various remote sensors for evaluating ecosystem processes has been the subject of a number of planning documents for the National Aeronautics and Space Administration (NASA) (NASA 1983, NASA 1984). Space-age technology may open avenues for testing many ecological hypotheses on regional and larger scales. In this article we describe some ecosystem variables that are precursors of change and indicate the potential of remote sensing for assessing these variables.

## Changes in net photosynthesis and transpiration

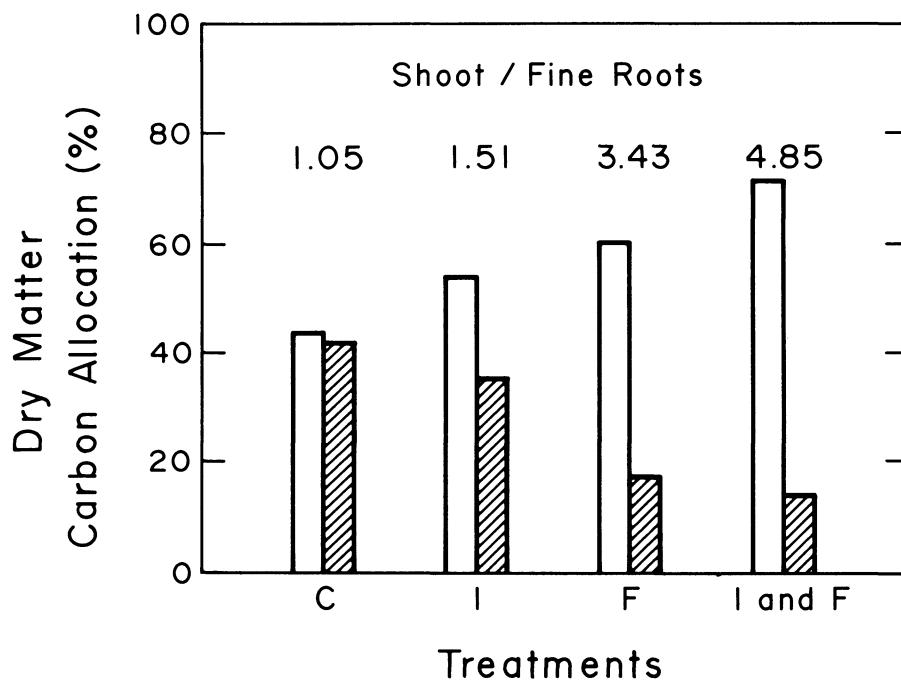
Logically, we should attempt to link absorbed radiation to canopy photosynthesis (Gallo et al. 1985, Hatfield 1984). Seasonal changes in canopy greenness have already been remotely sensed and reported for Africa (Tucker et al. 1985), North America (Goward et al. 1985), South America, and Asia (Justice et al. 1985) using a normalized near-infrared (0.73–1.1  $\mu\text{m}$ ) to red (0.55–0.68  $\mu\text{m}$ ) reflectance ratio of data collected by National Oceanic and Atmospheric Administration (NOAA) weather satellites (Yates et al. 1986).

For many annual crops, dry matter production, as well as photosynthesis, correlates closely with the amount of photosynthetically active radiation (0.4–0.7  $\mu\text{m}$ ) absorbed by a changing canopy throughout a growing season (Monteith 1977). Stresses of various kinds reduce the concentration of chlorophyll pigment, resulting in less absorption in the red wavelength region (0.55–0.68  $\mu\text{m}$ ) and a characteristic shift in the spectral reflectance curve (Goetz et al. 1983, Horler et al. 1983, Schwaller et al. 1983). Damage to chloroplasts also results in increased chlorophyll fluorescence, which can be estimated as alterations in the normal solar radiation spectrum above vegetation (McFarlane et al. 1980) or by laser-induced fluorescence (Brach et al. 1977, Chappelle et al. 1985).

Photosynthesis by perennial vegetation is often temporarily restricted by freezing, soil drought, and low atmo-

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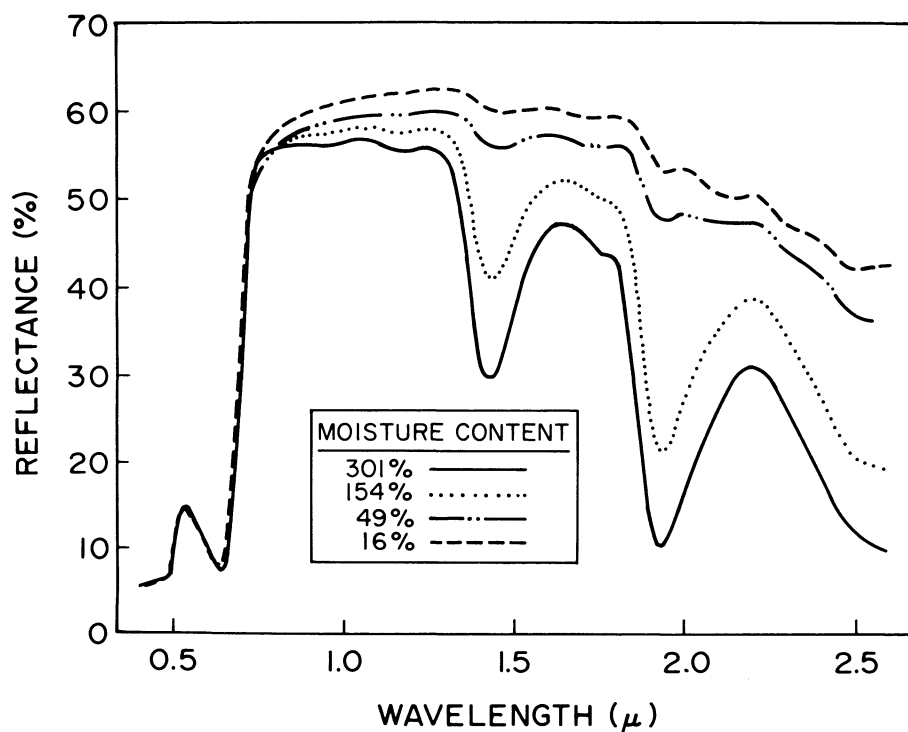
**Figure 1.** When pine trees in Sweden were irrigated (I), fertilized (F), or received both treatments (I and F), they allocated increasing proportions (1.05 to 4.85) of carbon into shoots (clear bar) vs. fine roots (cross-hatched bar) compared to untreated trees (C). Data from Axelsson (1981), drawing from Waring and Schlesinger (1985).

spheric humidity. Because these environmental conditions cause partial or total closure of stomata on leaf surfaces, they restrict transpiration as well. As a result, neither photosynthesis nor transpiration relates directly to increasing absorption of radiation by the canopy (Beadle et al. 1985, Berry and Downton 1982, Jarvis and Leverenz 1983). Moreover, when nutrient and water supplies are less than optimal, the proportion of growth that goes into roots may increase (Figure 1). For these reasons, the measured aboveground production of perennial plants is sometimes poorly related to the radiation intercepted by the canopy.

Assuming sensors were available that monitored canopy radiation absorption over the full photosynthetic spectrum, we might still overestimate photosynthetic activity if satellite information were analyzed only on clear, cloudless days. If a significant proportion of days are cloudy, photosynthetic activity should be reduced accordingly. Freezing temperatures, either at night or during the day, also pose a major constraint. Temperature can be estimated by monitoring emission in the long-wave, thermal infrared portion of the spectrum (8.2–12.2  $\mu\text{m}$ ) (Idso 1982, Smith et al. 1981). Temperature information may also aid in estimating stomata control on transpiration, particularly for short vegetation (Jackson 1982).

Extremely dry air can likewise limit leaves' ability to photosynthesize or transpire on bright, clear days. Although humidity cannot yet be measured directly, humidity deficit can be approximated throughout the day from minimum night (assumed dew-point temperature) and maximum day temperatures (Riha and Campbell 1985). Sustained drought may limit water uptake by plants and eventually halt photosynthesis if leaf water content (actually turgor) drops below a certain threshold. Decreases in leaf water content result in greater reflectance, particularly in the water-absorbing spectra between 1.3–1.6  $\mu\text{m}$  and 1.8–2.2  $\mu\text{m}$  (Figure 2).

Maintenance respiration also increases as perennial vegetation grows taller and the number of living cells in nonphotosynthetic tissues increases with elongation of conducting tissues serving roots and leaves. These non-



**Figure 2.** Spectral reflectance from sycamore leaves illustrates that changes in water content can be detected in the 1.3–1.6 and 1.8–2.2  $\mu\text{m}$  wavebands. Measurement of water content in living tissues (bottom two curves) requires high precision, unlike lethal water content (top two curves). After Rohde and Olson (1971).

photosynthetic cells require carbon resources for maintenance that might otherwise go toward growth (Figure 3).

How well photosynthesis and transpiration can be estimated from seasonal analyses of absorbed radiation and supplemental data representing constraints associated with cloudiness, temperature, drought, and humidity stress is not known. Estimating net photosynthesis appears feasible because the simple product of canopy leaf area and growing season length already correlates well with estimates of total carbon uptake by a wide variety of broadleaf forests (Figure 4). The related approach for estimating transpiration from satellite spectral data is discussed by Sellers (1985).

### Patterns of carbon allocation

As the availability of essential resources changes, so does the allocation pattern by which photosynthate is distributed within a plant to shoots, roots, reproductive organs, storage compounds, and defensive structures (Mooney and Chu 1974; see also Figure 1). In growing plants, the relative availability of carbohydrates and nitrogenous compounds in expanding tissue often mirrors the partitioning of carbon resources between roots and shoots (Lainson and Thornley 1982). Increasing nitrogen availability raises the protein content of foliage, whereas a reduction in nitrogen increases secondary wall thickening and lignification. In willow clones, for example, increases in foliar lignin to protein ratios induced under controlled conditions resulted in a proportional change in root/shoot production (Waring et al. 1985). Storage carbohydrates, such as starch, and defensive compounds, such as tannins and phenolics, also varied predictably as the availability of light and nutrients affected the carbon and nitrogen supply of expanding foliage. In a variety of vegetation types, the relative availability of nutrients and carbohydrates in the canopy also affects the nutritional quality of leaves for many animals and thus the potential for defoliation by herbivores (Coley et al. 1985, Gartlan et al. 1980).

Whether important biochemical features of canopies can be evaluated routinely from satellites is still unknown. Many biochemical com-

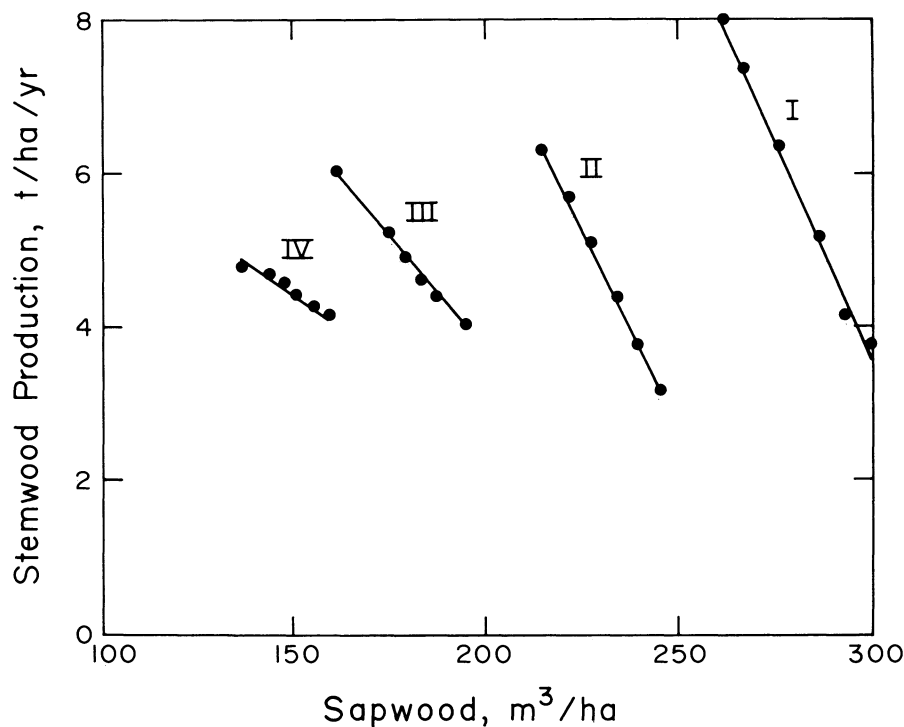


Figure 3. Stem growth of pine forests in Norway reaches a maximum on good (I) or poor (IV) sites after about 40 years, corresponding with maximum canopy development and net photosynthesis, denoted by the highest point for each site class. Thereafter, stem growth decreases in proportion to the increase in volume of living cells in the stem. Data from forestry yield tables of Brantseg (1969), analysis by Waring and Schlesinger (1985).

pounds have unique spectral absorption properties in the near-infrared range from 1.0 to 2.6  $\mu\text{m}$  (Figure 5). With sensors able to discriminate at 0.003- $\mu\text{m}$  resolution (Ferns et al. 1984), predictions based on laboratory spectral analyses of starch, protein, and lignin approach the precision of wet chemistry (Peterson et al. 1985, Spanner et al. 1985). Airborne measurements made five kilometers above hardwood forests indicate good correlations with leaf nitrogen content at specific wavelengths (Spanner et al. 1985; Figure 6).

Even in a vegetation type that maintains a relatively constant canopy from year to year, environmental conditions may vary sufficiently to affect growth in stem biomass. Average production or standing biomass may be correlated with the normalized near-infrared to red reflectance ratio generated from a variety of vegetation (Goward et al. 1985, Tucker 1980). A more general approach may be to use microwave (Hoekman 1985) or laser systems (Maclean and Krabill 1986, Nelson et al. 1984, Schreier et al. 1985) to assess changes

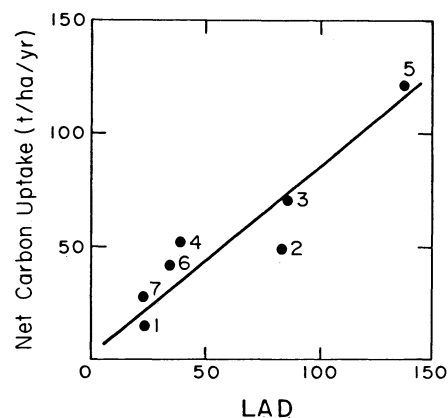
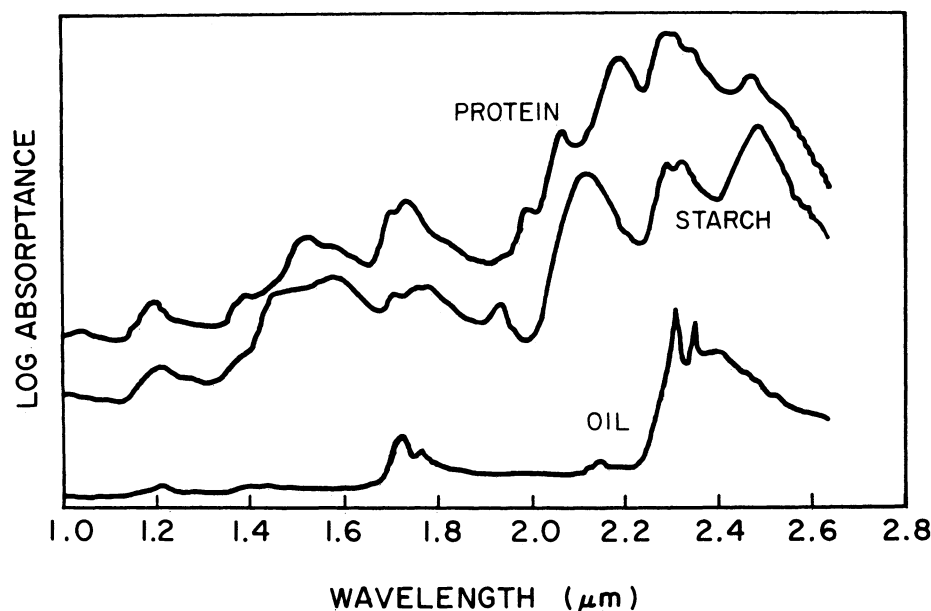
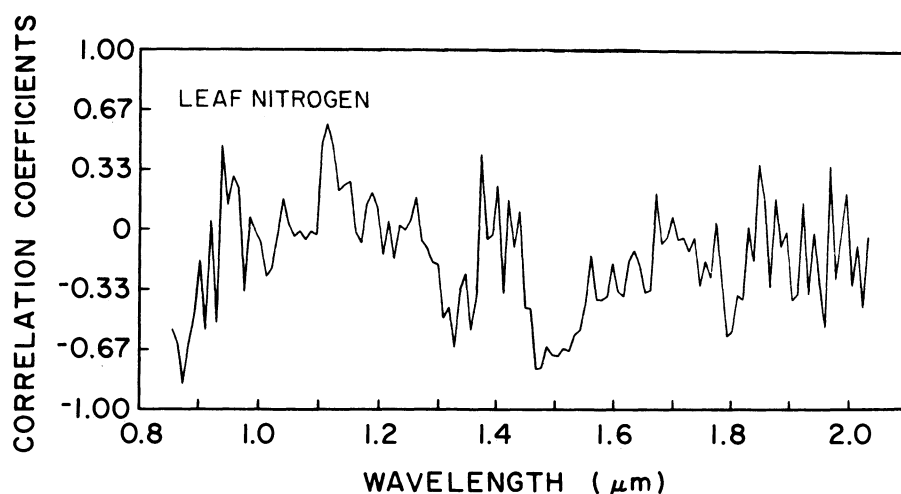


Figure 4. Net carbon uptake in a wide range of broadleaf forests increases as the product of leaf area index and number of months in the growing season increases. This index is termed leaf area duration (LAD). The numbered points refer to (1) *Fagus* forest in Japan, (2) *Castanopsis* forest in Japan, (3) broadleaf forests in Japan, (4) tropical humid forests of the Ivory Coast in Africa, and (5) tropical forests of southern Thailand (Kira and Shidei 1967). Point (6) is a *Liriodendron* forest in the southeastern United States (Harris et al. 1975), and (7) is a mixed hardwood forest from the northeastern United States (Whittaker et al. 1974). Drawing modified from Waring and Schlesinger (1985).



**Figure 5.** The absorbance spectra for pure samples of protein, starch, and oils in leaf tissue differ significantly from one another. Lignin, not shown, differs from starch and protein by absorbing more at 1.143, 1.417, and 1.446  $\mu\text{m}$ . After Rotolo (1979).



**Figure 6.** Spectral correlogram for nitrogen concentration in leaves ( $\text{mg}/\text{cm}^2$ ) of a hardwood forest in Wisconsin, derived from measurements taken 5 km above the canopy with an airborne imaging spectrometer. After Spanner et al. (1985).

in stem biomass at 1–5-year intervals.

If annual changes in aboveground production could be estimated independently from canopy properties, we would have an alternative to ground measurements for gauging the reliability of canopy biochemistry and estimates of photosynthetic activity in predicting the resources available for stem and branch growth. The ratio of net stem or aboveground growth to canopy photosynthesis may by itself prove a sensitive indicator of stress

because growth in stem mass has generally low priority in trees (Waring 1983) as well as in annual vegetation (Donald and Hamblin 1976).

### Plant maintenance respiration

Increases in the living portion of stem biomass, when not associated with corresponding increases in photosynthetic activity, can account for major reductions in annual production (Figure 3). The rate at which production

decreases should be a function of temperature. Scot pines growing on poor (class IV) sites in Norway are situated at higher elevations or latitudes than pines growing on good (class I) sites. Accordingly, production decreases more rapidly on the warmer (class I) than on cooler (class IV) sites.

Maintenance respiration can be expected to increase in proportion to the enzymatic (protein nitrogen) content of tissue. A doubling in protein N can double the maintenance cost (Amthor 1984, Penning de Vries 1975, Waring et al. 1985).

If remote sensing indicated significant increases in either canopy temperature or nitrogen content, we should expect decreases in aboveground production, assuming no measurable increase in photosynthesis or reduction in the proportion of resources allocated belowground to roots.

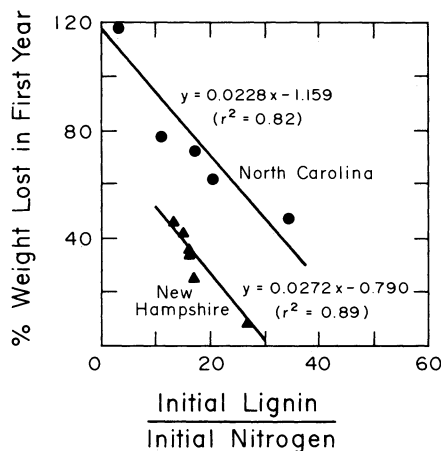
### Organic matter turnover

Leaf litterfall can be estimated by comparing annual extremes in canopy greenness or leaf area index. The near-infrared to red reflectance ratio of vegetation may fulfill this requirement (Running et al. 1986, Tucker 1980).

The ratio of lignin to nitrogen in litter is a sensitive indicator of how decomposition rates might be expected to vary in a given climate (Figure 7). Other elements such as phosphorus, known to be limiting in the tropics, might also be measured remotely in green leaves in the canopy (Peterson et al. 1985). Even if we could not predict retranslocation of nitrogenous and other materials from leaves before they fall, a significant change in lignin to nitrogen content of fresh foliage would suggest a corresponding change in decomposition of the material when it becomes detritus. A major change in decomposition rates could dramatically affect the release of various nitrogenous and sulfur compounds to the atmosphere and surface waters (Delwiche et al. 1978, Vitousek 1983).

### Conclusions

Plant canopies can give clues to ecosystem properties that might be pre-



**Figure 7.** Decomposition of leaves, as measured by weight loss, decreases progressively as the fraction of lignin/nitrogen increases. Decomposition is about 50% faster in North Carolina than in New Hampshire because of differences in temperature. After Melillo et al. (1982), redrawn by Waring and Schlesinger (1985).

cursors for a major change in structure and species composition. With a variety of remote sensing systems, it may be possible to estimate relative changes in the rates of basic processes such as photosynthesis, transpiration, maintenance respiration, and litter decomposition. In addition, if protein, starch, lignin, and other chemical constituents could be remotely sensed with sufficient precision, specific biochemical ratios could be used to interpret changes in allocation patterns affecting root growth and the susceptibility of vegetation to a variety of possible herbivores and pathogens.

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