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TESTING A THEORETICAL CLIMATE–SOIL–LEAF AREA HYDROLOGIC EQUILIBRIUM OF FORESTS USING SATELLITE DATA AND ECOSYSTEM SIMULATION

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ABSTRACT

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We hypothesize that a necessary equilibrium exists between climate, soil water-holding capacity and maximum leaf area in water limited coniferous forest ecosystems. To test this hypothesis over a large range of forests in Montana, spectral reflectance data from two different satellite sensors, Landsat/Thematic Mapper and NOAA/AVHRR, were combined with leaf area index (LAI) measured or simulated from a forest ecosystem model, FOREST-BGC. Transpiration simulated by the model with representative climatic and soil data was used to calculate equilibrium leaf area index of 20 mature conifer forest stands across Montana. A strong correlation was found between calculated and field measured of leaf area index, $R^2=0.87$. To test if satellite data can estimate LAI, measured leaf area index was correlated with spectral reflectance data from TM computed as the Normalized Difference Vegetation Index (NDVI) for 17 stands ($R^2=0.58$). Then, LAI for 53 conifer stands across Montana was estimated using our equilibrium concept and related to AVHRR/NDVI at 1.1 km scale ($R^2=0.88$). Species composition was found to be important only at the TM pixel scale of 30 m. AVHRR/NDVI provided an initial validation of our hydrologic equilibrium theory at regional scales. A quantitative relationship between climate defined simply as precipitation/potential evaporation, soil water-holding capacity and leaf area was developed using the model simulations. This relationship allows the prediction of either equilibrium leaf area index or soil water-holding capacity if the other is known.

INTRODUCTION

Leaf area index (LAI), the ratio of leaf area per unit ground area, is probably the most useful single structural variable for quantifying the energy and mass exchange characteristics of a terrestrial ecosystem. LAI is frequently used for estimating evapotranspiration and net primary productivity, variables directly related to such important issues as climatic change and global carbon cycles (Sellers et al., 1986).

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Of the many important variables that regulate leaf area displayed by the earth's vegetation, water availability is by far the most significant. More than 70% of the earth's vegetation at one time or another undergoes water stress. In arid and semi-arid climates, availability of water dictates the type and density of leaf area seen across the landscape. Climate provides water through precipitation, whereas, soil stores the water and makes it available to leaf area for transpiration. As a consequence of this supply-storage-demand interaction, an equilibrium should exist between the climate, soil, and leaf area in water-limited natural systems (Grier and Running, 1977; Eagleson, 1982). Assuming such an equilibrium exists in water-limited conifer forests of the northern Rocky Mountains, it should be possible to infer rational estimates of leaf area with prior knowledge of soil and climatic conditions. This study explores this ecological equilibrium concept for estimating LAI of mature conifer forests.

Research in tree physiology and systems modeling over the last decade has produced process level models relating transpiration and photosynthesis rates to local environmental conditions (Sinclair et al., 1976; Running, 1984). These ecosystem models, built on the concept of the soil-plant-atmosphere-continuum, can provide rigorous estimates of tree or stand water balance. For mature coniferous forests in Oregon, Grier and Running (1977) and Gholz (1982) found a strong relationship between stand leaf area and site water balance. Therefore, ecosystem models may be able to test the validity of our hypothetical hydrologic equilibrium between climate, soil and leaf area.

Advances in satellite remote sensing technology in the last decade offer a new tool for measuring terrestrial vegetation. Remote sensing techniques have been successfully used for vegetation classification on local, regional and global scales (Tucker et al., 1985; Goward et al., 1985; Justice et al., 1985). Combinations of red and near-infrared reflectances measured by satellite based sensors have been found to be strongly related to canopy characteristics such as LAI and biomass in various biomes (Wiegand et al., 1979; Peterson et al., 1987; Asrar et al., 1984). Remote sensing, by its dynamic and synoptic nature, provides complete spatial coverage at different spatial and temporal resolutions, thus eliminating the need for extrapolations. Such remotely sensed LAI may provide a rapid validation of the existence of a hydrologic equilibrium over large areas of diverse climate and soils.

This study has the following objectives: (i) to test the existence of a hydrologic equilibrium on a local scale; by estimating leaf area index of mature conifer forest stands using an ecosystem model and comparing with field measured LAI and (ii) to test the validity of the hydrologic equilibrium on a regional scale; by estimating LAI of mature conifer forests and comparing with satellite data.

The objectives were approached by first, estimating equilibrium LAI using an ecosystem model and relating the estimated LAI with LAI measured on 20 field sites. Then as a test of satellite data for estimating LAI, we related measured LAI to spectral reflectance data from Landsat/Thematic Mapper. Finally for testing the hydrologic equilibrium on a regional scale, we estimated equilibrium LAI for 53 mature conifer forest stands across western Montana using the ecosystem model and related the estimated LAI to spectral reflectance data from the NOAA/AVHRR.

RELATION BETWEEN CLIMATE-SOIL-LEAF AREA INDEX

Vegetation in a given area is an integrated measure of its environment and history. Terrestrial ecosystems survive and flourish by adapting to the environment through changes in species composition, morphology and physiology within a species, and canopy density or leaf area within the plant community (Larcher, 1980). It is well known that stand leaf area decreases where water is limited. Both climate and soil play a significant role in determining the water availability of a site. The climate of the northern Rocky Mountains is characterized by a relatively rainless period of varying duration and drought severity beginning in June and ending in October. This period corresponds to approximately 80% of the growing season for forests in this region. Thus, water required by forests for growth and survival through summer is mainly provided by water from snow melt in the soil at the beginning of the growing season. As a consequence of this precipitation pattern, many coniferous forests in this region undergo moderate to severe water stress in mid-to-late summer (Donner and Running, 1986). The amount of water retained in the soil, from spring snow melt, is a function of soil texture and depth. As a result, the soil hydrologic property, available water capacity (water held between field capacity and "permanent wilting point") plays a significant role in determining forest growth. Climate also influences vegetation through evaporative demand, which usually exceeds available water during the growing season. Therefore, trees must strike a balance between maximizing photosynthesis and maintaining a suitable internal water status. Increasing leaf area would increase photosynthetic potential, but at the cost of increased transpirational water loss. A negative feedback between transpiration and stomatal aperture exists to restrict water loss and the further development of water stress, but at the cost of reduced CO_2 fixation. Tissue water content of established conifer trees is apparently maintained at levels > -2.0 MPa at which point stomata are closed continuously. As a result, where available soil water and stomatal control are insufficient to maintain internal water potential of trees above -2.0 MPa, stand leaf area must reach a new balance. Short term adjustments of leaf area may result from a variety of factors including changes in needle morphology due to water stress (Richter, 1974) or premature senescence and loss of lower branches and older needles due to high water stress. However, long term adjustments of leaf area are probably achieved from mortality of less competitive individuals.

METHODS

Site and stand measurements

Western Montana is characterized by a cool, dry climate during the growing season. Average annual precipitation ranges from 250 cm in the northwest to 35 cm in southwest parts of the region. More than 50% of the total precipitation is received as snowfall during the winter months. The vegetation is predominantly evergreen forests; the growing season defined by air temperature, $> 0\,^\circ C$, starts in early March and extends to the end of October.

Study sites were located across western Montana to capture the climatic diversity in this region. Forest stands in these locations were carefully chosen to be 50 years or older. There is good evidence that leaf area of forest communities reaches a more or less steady-state early in succession (Kira and Shidei, 1967; Marks and Bormann, 1972). Stands with diseases and pests or other form of disturbance often may not reflect potential abiotic limits for growth, so were eliminated. Twenty stands for which field LAI measurements were available from previous studies were chosen for estimating steady-state LAI using our equilibrium concept. Some biophysical characteristics of these stands are given in Table 1. Only 17 of the 20 stands were used for relating estimated LAI to spectral reflectances from the Thematic Mapper, as three stands were outside our Thematic Mapper scene. Major forest species encountered on the sites were *Pseudotsuga menziesii* Franco, *Pinus contorta* Dougl., *Pinus ponderosa* Laws, *Larix occidentalis* Nutt, *Abies grandis* Lindl. Fifty-three stands across western Montana, representing mature, undisturbed coniferous forests, were selected for testing our equilibrium concept on a regional scale using satellite data from NOAA/AVHRR. These 53 stands, chosen using aerial photographs, were selected to represent a variety of combinations of climate and soil conditions that support conifer forests.

Lead area index for each stand was calculated using species specific allometric equations. These equations relate sapwood area of the trees to the total foliage biomass. Foliage biomass was then converted to leaf area using surface/mass conversion factors. Details of this methodology were given in McLeod and Running (1988) and Peterson et al. (1987). Projected LAI used in the analysis was computed by dividing total LAI by 2.5.

The only site parameter required was available soil water capacity, defined as soil water content from -0.01 to -1.5 MPa. The Soil Conservation Service (SCS) produced maps of soil series along with data on texture, depth, and available water capacity (AWC) for this region. For each stand information on AWC and depth was extracted from the soil series maps. The AWC was adjusted to total AWC based on soil depth. The maximum depth was restricted to 100 cm, as the majority of roots occur within the first 100 cm of soil. For six of the 20 stands AWC was directly measured for another study using pressure

TABLE 1

Biophysical characteristics of forest stands

Site	Dominant tree[a] species	Projected LAI (measured)	Soil water capacity (cm)		Base met. station
			(measured)	(estimated)	
Noxon	PP	3.36	29.6	30.0	Trout Creek
Troy	PP	2.92	21.6	20.0	Troy
Sloway	PP	2.08	12.8	15.0	Superior
Plains	PP	2.60	20.0	18.5	T-Falls
Edith	PP	2.16	18.8	21.0	Missoula
Sorrel	PP	2.76	23.1	21.0	Missoula
Sec. 31	DF	2.36		13.5	Lubrecht
Elk Cr S	DF	1.92		11.5	Lubrecht
Elk Cr N	DF, LP	2.04		16.2	Lubrecht
Nine Mile	PP	1.60		13.2	Lubrecht
Case Ranch	PP	1.68		13.2	Lubrecht
Placid Lk	DF, LP	3.04		22.0	Seely
Rainy Lk	DF, PP	4.00		33.0	Condon
Lake Inez	PP	1.84		15.0	Condon
Lake Alva	L, PP, GF	3.56		25.0	Condon
Condon	PP, LP, DF, L	2.72		18.0	Condon
Kraft Cr	PP	2.36		17.5	Condon
Jim Cr	L, PP, DF	3.60		29.0	Condon
Donlan	LP, PP	2.20		22.0	Superior
Morrison	LP, PP	1.62		14.0	Lubrecht

[a]PP=ponderosa pine, DF=douglas fir, LP=lodgepole pine, L=western larch, GF=grand fir. Data for the first 6 ponderosa pine stands was obtained from McLeod and Running 1988.

plate technique in the laboratory (McLeod and Running, 1988). The relation between measured and estimated (SCS) available water capacity (cm) for the six stands was: $AWC_{obs}=1.03AWC_{est}-0.65$; $R^2=0.87$; $SE=2.2$ cm.

Data used for validating the soil moisture extraction and leaf water potential patterns produced by FOREST-BGC were obtained from two previous studies conducted at the University of Montana, School of Forestry, Lubrecht Experimental Forest in 1983 (Donner and Running, 1986; Potts, 1986). Both studies explored the effects of thinning on soil moisture extraction and tree water relations of lodgepole pine stands. Measurements of soil moisture extraction for the thinned and unthinned stands were obtained at weekly intervals using a neutron probe. Pre-dawn leaf water potentials were measured using the pressure bomb technique. Total leaf area index of the lodgepole pine stands was found to be 3.5 and 5.1 for the thinned and unthinned stands respectively (Donner and Running, 1986). Available water capacity was estimated to be 20 cm in the top 100 cm, while field capacity was 30% by volume. Meteorological data to run the model were collected from the Lubrecht Expt. Forest central meteorological station less than one km away from the stands.

Ecosystem model – FOREST-BGC

FOREST-BGC is a process level ecosystem simulation model that calculates the cycling of carbon, water and nitrogen through forest ecosystems (Running and Coughlan, 1988). The model requires daily input data of standard meteorological conditions: maximum and minimum air temperature, dew point, incident shortwave radiation, precipitation and definition of important site and vegetation variables: soil water-capacity and leaf area index. The model calculates key processes of canopy interception and evaporation, transpiration, soil outflow of water; photosynthesis, growth and respiration, allocation, litterfall, and mineralization of nitrogen. The model has a mixed time resolution, with hydrologic, photosynthetic and maintenance respiration processes computed daily, and the other carbon and all nitrogen processes computed yearly.

For this study the important parts of the model are seasonal transpiration, evaporation and canopy water stress. Briefly, daily precipitation is routed to snowpack or soil dependent on air temperature, a canopy interception fraction based on LAI is subtracted and evaporated, and remaining water goes to a soil compartment where it is available for transpiration. Transpiration is calculated with a Penman–Monteith equation incorporating vapor pressure deficit and incident radiation as driving variables. Air temperature below 0°C reduces canopy conductance to cuticular values, and is an important determinant of the growing season length. Canopy conductance is linearly reduced to a default cuticular value when either average daily vapor pressure deficits exceed 16 mb or pre-dawn leaf water potential, estimated from soil water-availability, decreases below -1.65 with a lower limit of -2.0 MPa. Aerodynamic conductance is fixed at 0.2 m s^{-1} in the Penman–Monteith equation.

Because the primary interest in this study is transpiration, only the daily half of the model was used. Further, simulations were run only for the period between April 1 and October 31.

Climatic data for the model

Climatic data from National Weather Service records for the year 1983 were chosen as inputs to the model, because weather patterns during 1983 were similar to the long-term conditions for this region. Precipitation deviated by less than 10% and temperatures were within 1°C from long-term averages. For each site, maximum and minimum temperatures and precipitation data were retrieved from records at the nearest weather station (base station). To produce site specific meteorological data for each of the stands, the base station data were processed through a mountain microclimate simulator, MT-CLIM

(Running et al., 1987). MT-CLIM uses climatological principles to extrapolate base station data to produce site specific conditions of incident solar radiation, daylight average temperature, minimum temperature, daylight average relative humidity and daily total precipitation.

MT-CLIM uses the Bristow and Campbell (1984) procedure for estimating daily solar radiation at the base station: first, potential incident solar radiation to a flat/slope surface is calculated using sun–earth geometry. Then an atmospheric transmission coefficient is computed based on site elevation and a seasonally corrected cloudcover calculated from daily temperature amplitude. Finally, daily potential radiation is multiplied by the atmospheric transmission coefficient to give actual incident solar radiation. Running et al. (1987) found that the procedure gives reasonable estimates of daily solar radiation in this region.

Site specific temperatures are produced by adjusting base station temperatures based on topographic variables: slope, aspect and elevation and canopy cover. Extrapolated air and dew point temperatures are used to compute relative humidity. When dew point temperatures are not available at the base station, night minimum air temperatures are substituted (Running et al., 1987). Base station precipitation was adjusted using isohyetal maps to give site precipitation.

Water equivalent snowpack data is very critical to begin model runs, as a major portion of the hydrologic cycle is driven by snow in this region. Average depth of snowpack for yearday 91 were obtained from Soil Conservation Service (SCS) snow surveys. Again the data were adjusted for each stand based on the differences in slope, aspect, elevation and canopy density between the stand and location of the snow measurements (Parker, 1971; Hendrick and Filgate, 1971). For example, on steep south-facing slopes snow melts at a higher rate than on a north facing slope, because of differential radiation input, so these sites were defined with lower initial snowpack on yearday 91.

Procedure used for estimating equilibrium leaf area index

Transpiration integrates soil water availability and the atmospheric evaporative demand, and has a great influence on physiological processes that determine growth. This application required that the model be initialized with known equilibrium conditions. From previous work, it was found that, with a soil water capacity of 23.5 cm, a site can support an LAI of 6.0 with a summer minimum pre-dawn leaf water potential of -1.5 MPa, for the prevailing climatic conditions at Lubrecht Experimental Forest, Montana (Running, 1984; Graham and Running, 1984; Hungerford, 1987; McLeod and Running, 1988).

The above conditions at Lubrecht were chosen as the base model run against which all other runs were compared. By changing soil and climatic conditions the model produces transpiration that may be higher/lower than that of the base run. If maximum water stress is fixed at -2.0 MPa, an increase in simulated transpiration from base run implies an increase in leaf area carrying capacity of the site and vice versa. Therefore, it was hypothesized that the differences in transpiration between base and other simulations are directly proportional to the differences in leaf area of forest stands. Finally, the simulated transpiration (TRAN) at different sites was converted to leaf area index values using the proportionality

$$\frac{TRAN_{site}}{TRAN_{base}} = \frac{LAI_{site}}{LAI_{base}} \tag{1}$$

Remote sensing data

Remote sensing data from a Landsat Thematic mapper overpass on July 18, 1984 were acquired. Sample stands were located by displaying the imagery on a color monitor, and the sample plots were found with the help of air photos. The reflectance vector for each sample plot consisted of mean digital numbers (DN) for a 3×3 matrix of pixels around the plot. The mean DNs were converted to radiance values based on the published gain settings. The radiance data were adjusted to differences in irradiance based on slope and aspect for each plot. No atmospheric corrections were attempted due to lack of adequate ancillary information, however atmospheric clarity is usually quite high in Montana.

For testing the relationship between estimated LAI and spectral reflectance on a regional scale, data from the NOAA-9/Advanced Very High Resolution Radiometer were acquired on September 25, 1985. The use of TM data from 1984 and AVHRR from 1985 should not influence results as leaf area index of mature coniferous forests does not change significantly from year to year (Waring et al., 1986). The local area coverage data after geometric corrections were used to locate and extract the DN values for each sample site. Again, no efforts were made to correct for atmospheric interference.

Spectral reflectances from TM and AVHRR were correlated with estimated LAI in the form of a ratio involving red and near-infrared (IR) wavelength bands. Previous research has established significant correlations between canopy properties such as LAI and IR/red combinations (Tucker, 1979; Asrar et al., 1984; Curran, 1983). The underlying principle for such a relationship is as follows: chlorophyll pigments in green leaves absorb radiation in the red wavelengths. Red wavelength is thus inversely related to the quantity of chlorophyll present in the canopy. On the other hand, near-infrared radiation is scattered by internal leaf structure, and is then either reflected or transmitted, allowing multiple layers of leaves to influence overall infrared reflectance.

In the present study we chose the most popular band combination, Normalized Difference Vegetation Index (NDVI) for relating leaf area index to spectral reflectance. Thematic Mapper/NDVI was computed as (band 4 − band 3)/(band 3 + band 4); where band 3 is from 0.63–0.69 μ, band 4 is from 0.76–0.90 μ. AVHRR/NDVI was computed as (band 2 − band 1)/(band 1 + band 2); where band 1 is from 0.55–0.68 μ, band 2 is from 0.72–1.1 μ.

Finally, a quantitative relationship was developed between available water capacity and leaf area of conifer forests for climates at three different locations in western Montana. The ratio of precipitation to potential evaporation (PE) was used to differentiate climates. PE was computed using the methodology reported by Linacre (1977) as follows

$$PE\ (\text{mm day}^{-1}) = \frac{700\ T_m/(100-A) + 15\ (T-T_d)}{(80-T)} \quad (2)$$

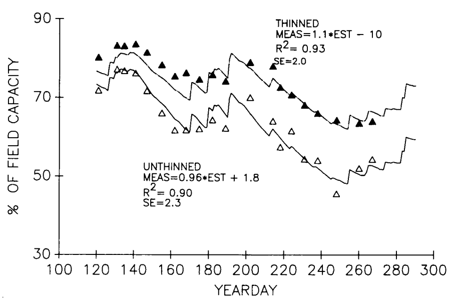
Where $T_m = T + 0.006h$, h is elevation (m); T = mean temperature; A = latitude; T_d = mean dew point temperature.

For each climate a relation between LAI and available water capacity was generated using the logic described earlier, changing the AWC by 5-cm intervals.

RESULTS AND DISCUSSION

Model validation

Figure 1 shows simulated and measured seasonal soil moisture extraction for thinned and unthinned lodgepole pine stands. The agreement between measured and simulated values is strong, where, Y is measured and X is sim-



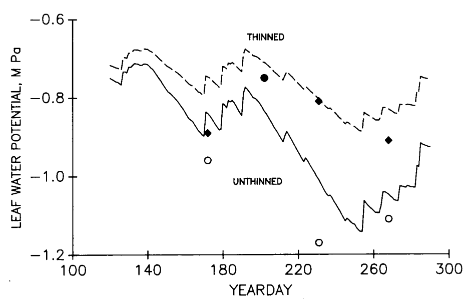


Fig. 1. The seasonal trends of soil moisture extraction simulated by FOREST-BGC (line) compared to neutron probe measurements (symbol) for thinned and unthinned lodgepole pine stands in Montana providing a validation of the model for simulating hydrologic balances. Neutron probe measurements are averages of five samples from 0–100 cm depth.

Fig. 2. The seasonal trends of pre-dawn leaf water potential simulated by FOREST-BGC (line) compared to pressure chamber measurements (symbol) for thinned and unthinned lodgepole pine stands in Montana providing a validation for the model for simulating canopy water stress. Pressure chamber measurements are averages of five trees, from Donner and Running (1986).

ulated soil moisture extraction, $Y=0.96X+1.8$; $R^2=0.90$ for unthinned, $Y=1.1X-10.0$; $R^2=0.93$ thinned stand. The model also predicted seasonal trends in water stress measured as pre-dawn leaf water potentials to within -0.15 MPa (Fig. 2). In previous studies, an earlier version of the model was also found to give good estimates of seasonal pre-dawn leaf water potentials and stomatal resistance (Graham and Running, 1984; Running, 1984). We feel FOREST-BGC, can be used to characterize and quantify expected differences in water budgets between different sites, and provide a crucial tool for exploring our ecological theory of the climate and soil control of equilibrium leaf area. This model has a decisive advantage over conventional methods of water budget computation (Grier and Running, 1977; Eagleson, 1982), as it allows for physiological controls over water loss and better hydrologic partitioning.

Relation between measured and simulated LAI

Field measurements for the 20 stands found LAI ranged between 1.5 and 4.0 (Table 1). Figure 3 shows the relation between simulated and measured leaf areas for the 20 mature coniferous forest stands. There is a strong linear relationship between LAI simulated from eq. 1, (X), and measured LAI (Y); $Y=0.86\,X+0.4$ with R^2=0.87. McLeod and Running (1988) reported similar results for ponderosa pine. The evidence from these results suggests that the relationship between leaf area and site water balance is species independent, justifying this model application without species specific tuning of physiological response parameters. Grier and Running (1977) also reported a species independent relationship between site water balance and stand leaf area for mature conifer forests in Oregon. They concluded that while the ability to exert physiological control over water loss may be a principal factor in determining which species will contribute to community leaf area, the physical water balance dictates the potential leaf area for that community. Running (1976) re-

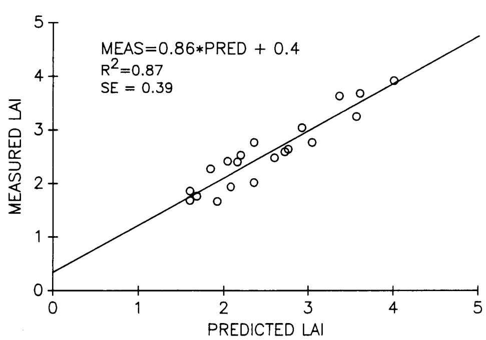


Fig. 3. The relation between measured and simulated LAI for 20 mature coniferous forest stands in western Montana. Simulated LAI data were derived from seasonal transpiration computed by FOREST-BGC with site specific soil and climate data. See eq. 1 and Table 1.

ported that stomatal control of transpiration provides a fairly narrow range of adaptation within a species. Consequently, the strong relation between measured and simulated LAI confirms the significant control water-availability exerts on leaf area carrying capacity of forest stands in water limited regions like the northern Rocky Mountains.

Another important reason for the strong linearity may be that transpiration increases linearly up to a projected LAI of 4–5 (Larcher, 1980). Short growing seasons along with low summer precipitation in this region are not very conducive to the development of leaf area above 4–5. Beyond an LAI of 5, radiation becomes limiting for photosynthesis in the lower canopy layers. Short-term adjustments in leaf area are usually achieved by a self pruning process of lower branches.

The slight overestimation in simulated LAI may have been due to the role of understory in moisture extraction, which was not accounted for in the present study. The use of eq. 1 for the stands differing in species composition from the base model run (lodge pole pine) may not have contributed to significant error. Model simulations with measured LAI and soil data for the six ponderosa pine stands showed the error to be within $\pm 5\%$.

The methodology used in this study: using extrapolated meteorological conditions to simulate transpiration with measured/estimated soil data in association with a known equilibrium condition, seems to provide a useful tool for exploring the equilibrium condition between climate, soil, and leaf area. However, the relation found in this study may not hold under conditions of (i) severe nutrient deficiency; (ii) in areas where mechanical damage by wind or heavy snowfall reduced canopy biomass; (iii) damage due to pests, diseases, and predators and (iv) systems that are cultivated, irrigated or fertilized.

Remote sensing of leaf area index

Given the strong correlation between simulated and measured equilibrium leaf area, we studied the relationship between measured leaf area and spectral reflectance data from the Thematic Mapper to acquire evidence as to the usefulness of satellite data for validating our hydrologic equilibrium theory at larger spatial scales.

Thematic mapper

Figure 4 shows a log–linear relation between field measured LAI and the Thematic Mapper/NDVI for 17 conifer forest stands, $R^2 = 0.58$. When two of the 17 stands with more than 20% larch trees were excluded the R^2 improved from 0.58 to 0.80. The reason for this could be that larch is a unique deciduous conifer with significantly different spectral properties compared to all other native conifers. Our laboratory spectral analysis of conifer needles indicated

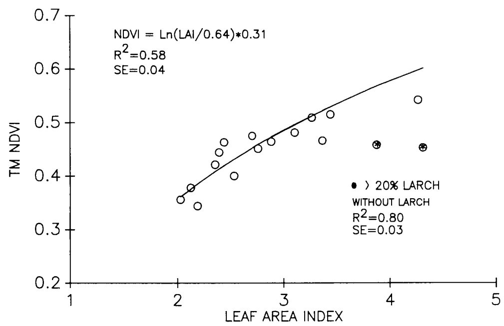


Fig. 4. The relationship between reflectance data from a Thematic Mapper overpass on July 18, 1984, measured as NDVI, ((IR − RED)/(IR + RED)) and measured leaf area index for 17 mature conifer stands. Exclusion of the two stands with more than 20% larch, a deciduous conifer, R^2 increases to 0.80.

that larch reflects 20% more in the red wavelength which results in lower NDVI values. Peterson et al. (1987) reported similar non-linear relationship between leaf area index and IR/Red ratio for conifer forests in Oregon using the Airborne Thematic Mapper Simulator done across a region with 12 different conifer species. They also reported better statistical results after atmospheric corrections; though the basic relationship did not change.

We conclude, along with previous research, that leaf area index of conifer forests can be estimated from satellite data. However, the results from our analysis point out the need for a knowledge of the optical properties of various species for estimating LAI from Thematic Mapper data.

Regional test of hydrologic equilibrium theory using AVHRR/NDVI

Given the evidence that equilibrium LAI can be estimated from model simulations and remotely sensed on a local scale, we went on to test the validity of our hydrologic equilibrium theory on a regional scale using 1.1 km NOAA/AHVRR data.

Figure 5 shows the relation between estimated LAI, from model simulations, and AVHRR/NDVI at 1.1 km scale for 53 sites across western Montana. A similar log–linear relationship emerged between the two variables, $R^2 = 0.88$ confirming the existence of a fundamental relationship between IR/red wavelength combinations and leaf area index of conifer forests. Presence of larch did not deteriorate the correlation, probably due to the broader wavelength bands and larger spatial resolution of AVHRR, where individual components of a scene can not dominate the spectral reflectance as much as at TM scale.

The relation shown in Fig. 5 seem to corroborate our ecological theory that climate along with soil water capacity controls the maximum leaf area index of a forest at regional scales also. The relation also provided evidence that LAI

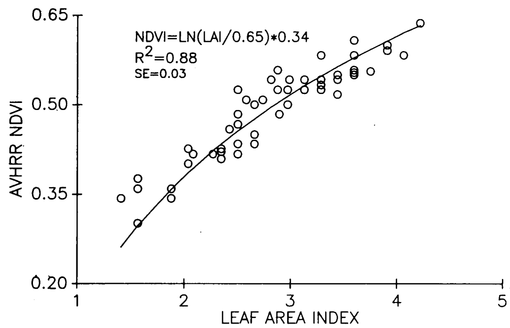


Fig. 5. The relationship between reflectance data from a NOAA/AVHRR overpass on September 25, 1985, measured as NDVI, ((IR−RED)/(IR+RED)), and estimated leaf area index for 53 mature conifer forest stands across western Montana. This relationship was developed to test our ecological equilibrium theory on a regional scale. Leaf area index was estimated using the forest ecosystem model, see eq. 1.

can be estimated from AVHRR/NDVI at large spatial scales for regional ecosystem analysis research.

A number of factors contributed to the strong relationship between estimated LAI and NDVI. From theoretical studies involving canopy radiation models the relationship between LAI and NDVI was found to be non-linear and depended on the optical properties and canopy architecture of the vegetation (Sellers, 1985). The canopy radiation models also predict the relationship to be linear up to an LAI of 3–4, and approaching an asymptote around a LAI of 6–7. The results from the present study seem to corroborate the theoretical findings, partly, because the range of LAI used was only between 1–5. Forest stands in western Montana, in general, seem to support a maximum LAI of 4–5; which may have contributed to the strong relationship between estimated LAI and NDVI.

Stands chosen in this study were extensive, homogeneous and usually with complete canopy cover, thus minimizing the contribution of understory and soil on spectral reflectance. Consequently, a strong correlation emerged between overstory LAI and spectral reflectance values. However, under other stand conditions such a relation may not be expected.

From our analysis, we conclude that satellite data provides a quick validation of our hydrologic equilibrium theory at various spatial scales. The ability to estimate LAI on a regional scale from satellite data is critical, because legitimate alternatives for estimating LAI at large spatial scales do not exist. The combination of satellite data and ecosystem simulation could be a useful package for analyzing the structure and function of ecosystems at spatial scales larger than can be measured directly.

Given that leaf area index can be estimated from remote sensing data; the equilibrium concept provided with climate data offers the possibility of infer-

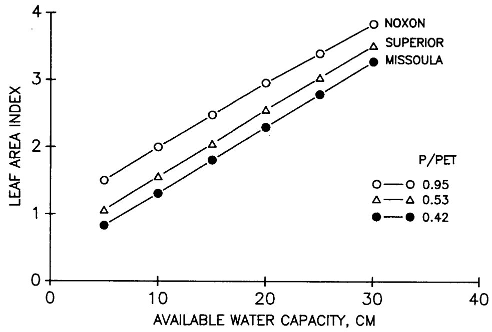


Fig. 6. Our hypothesized general relation between climate, soil available water capacity, and leaf area index for water limited conifer forests in western Montana. Three climates, Noxon, Superior and Missoula with varying degrees of climatic efficiency defined as the ratio of precipitation to potential evapotranspiration are represented. For each climate, the relation between projected LAI and soil available water capacity was derived from model simulations using FOREST-BGC.

ring general soil properties. Such a relationship between climate, soil (AWC) and leaf area from theoretical simulations is shown in Fig. 6 for climates at three different locations. As discussed earlier, in snowpack controlled water limited areas such as western Montana, soil hydrologic properties, more so than climate, control canopy development. However, for a given AWC the climate sets the upper limit of leaf area carrying capacity mainly through its influence on growing season length and evaporative demand during the growing season.

Knowledge about soil properties is difficult to obtain, yet is extremely important in various research activities. On a local scale, soil properties are important for predicting forest productivity, estimating water yield and run off (McLeod and Running, 1988; Burrough, 1983). At a global scale, the biosphere–atmosphere interactions were found to be highly sensitive to soil hydrologic properties (Wilson et al., 1987; Sellers et al., 1986). Soil characteristics are known to vary even on the scale of a hill slope. Consequently, defining soil properties appropriate for global climate models becomes extremely difficult. Upon further development and verification of relationships as shown in Fig. 6 for various biomes, it may be possible to make rational estimates of soil hydrologic properties at various scales using ecological theories along with remote sensing technology, a capability which should be of great use to ecologists, hydrologists and global climate modelers.

CONCLUSIONS

Evidence was provided that coupling satellite data with ecosystem simulation was a valuable tool for studying the interactions between climate, soil, and vegetation. The analysis illustrated the potential for using satellite data to describe the differences in leaf area index for regional ecosystem studies. LAI estimates from satellite based sensors may be used to provide more direct estimates of the carbon content and exchange rates of global vegetation than are possible with current data. The combination of ecosystem simulation with remote sensing may also provide insights into canopy dynamics such as carbon partitioning allowing the detection of ecosystems undergoing stress due to pests, diseases, and nutrients (Waring et al., 1986). Continued development of the combined use of satellite data with ecological theory should improve our ability to infer properties and fluxes of land surfaces from satellite data.

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