

# Developing remote sensing techniques to estimate photosynthesis and annual forest growth across a steep climatic gradient in western Oregon, USA

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## Abstract

Waring, R.H., Runyon, J., McCreight, R., Yoder, B., Goward, S.N. & Ryan, M. 1993. Developing remote sensing techniques to estimate photosynthesis and annual forest growth across a steep climatic gradient in western Oregon, USA. In: Management of structure and productivity of boreal and subalpine forests (ed. S. Linder & S. Kellomäki). *Studia Forestalia Suecica* 191. 94 pp. ISSN 0039-3150, ISBN 91-576-4822-0.

The upper limits to photosynthesis are set by the amount of light intercepted daily and annually by green foliage. Freezing temperatures, drought, and humidity deficits further constrain photosynthesis. The visible light intercepted and that utilized by forests distributed across an environmental gradient in western Oregon were assessed from ground-based meteorological and physiological measurements. Utilized light was converted into biomass increment and showed an annual efficiency of  $1 \text{ g MJ}^{-1}$  for forests with aboveground production from  $<2$  to  $17 \text{ Mg ha}^{-1} \text{ yr}^{-1}$  ( $r^2=0.98$ ). We present analogues in remote sensing for all of the ground-based measurements. We illustrate how various sensors estimate: (1) solar radiation, (2) temperature, (3) drought, (4) atmospheric water vapor deficits and (5) key properties of the vegetation. Combined, these remotely sensed techniques offer a means of estimating forest growth in the Pacific Northwest and possibly, globally.

*Key words:* light interception, photosynthesis, respiration, remote sensing, climate change, net primary production.

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MS. received 4 November 1992

MS. accepted 13 January 1993

## Introduction

Large changes in climate are predicted in the next century as a result of increasing production of greenhouse gases. Natural systems of the future are expected to differ structurally from those observed today. Given these uncertainties, by what means are we to evaluate the potential effects of climate change on vegetation? One benchmark for measuring change came in 1972 with the launching of the first in a series of Landsat satellites. Much greater coverage is

planned from a variety of satellites near the end of the present decade. With improvements in calibration, spectral sensitivity, spatial coverage, and data processing, new satellite sensors offer the potential to follow subtle changes in the biophysical characteristics of landscapes. We had the opportunity, as part of a NASA sponsored research project (Oregon Transect Ecosystem Research, OTTER), to investigate whether current remote sensing techniques

might be used to assess constraints on photosynthesis, transpiration, decomposition, and other related ecosystem processes. We assert that changes in essential ecosystem processes are potential forecasters of impending change in ecosystem structure.

In this paper we focus on estimating photosynthesis and growth. Current process models use detailed information on the physiological status and local environment to evaluate these variables daily, seasonally, and yearly (Running & Coughlan, 1988). In this study we seek to generalize for a wide range of species and to minimize the information required for seasonal integration. From ground measurements, we estimate the visible fraction of solar radiation intercepted by forest canopies and the constraints on utilizing the intercepted radiation due to freezing temperatures, drought, and high atmospheric vapor pressure deficits. We compare annual estimates of utilized radiation against measured growth as a validation of the concept. We also consider the need for additional information in estimating growth of very old forests. We then consider remote sensing analogues for all of the ground-based measurements, with the goal of using remote sensing alone to predict photosynthesis and growth at regional and global scales.

## Study area and measurements

The transect in Oregon (Fig. 1), is located near that established and described in detail by Gholz (1982). In June, 1989, we installed meteorological stations near the sites along the transect. The stations automatically recorded at hourly intervals: incoming short-wave solar radiation, air temperature, relative humidity, and precipitation. Descriptions of the vegetation and soils appear in Gholz (1982) and in Franklin & Dyrness (1973). We estimated standing woody biomass of trees from diameter measurements made within 20–50 circular plots (50 m<sup>2</sup>) using equations developed by Gholz, Grier, Campbell & Brown (1979). Annual aboveground growth was derived using the same biomass equations with diameter as the independent variable (Table 1). Diameter growth was measured on increment cores extracted from the 1st, 5th, and 10th tree of each species on each plot.

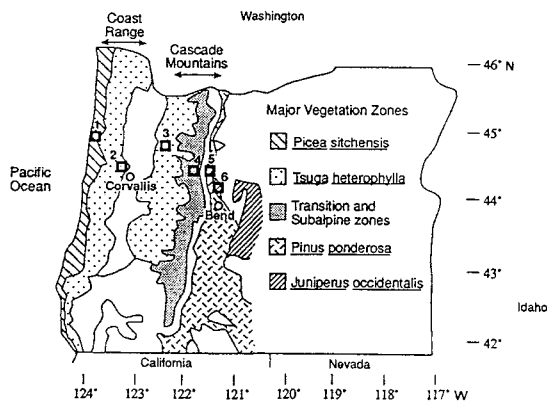


Fig. 1. Map of the study area in Oregon showing the location of meteorological stations (numbers 1–6) and major vegetation zones designated by the dominant tree species (after Gholz, 1982; Franklin & Dyrness, 1973).

At the time of maximum canopy development in July we measured intercepted photosynthetically active radiation (IPAR) with a Sunfleck Ceptometer as described by Pierce & Running (1988), (Table 1). The fraction of incident solar radiation intercepted by the conifer-dominated forests remained nearly constant throughout the year. The deciduous forest of alder (*Alnus rubra* Bong.) initiated new leaves in April and dropped most foliage by late October. Soil drought, as it limits water uptake and stomatal conductance, was assessed by measuring predawn water potentials of trees periodically throughout the dry season (Table 2). In addition, we periodically collected data on photosynthetic rates and stomatal conductance at sites 1, 2, 3 and 5 to confirm previous studies reported by Running (1976), Emmingham & Waring (1977) and Waring & Franklin (1979).

## Physiological analysis of climatic data

The upper limits on growth are established by the amount of photosynthate accumulated throughout the year, or carried over from the previous year (Hunt, Martin & Running, 1991). In many areas, intercepted photosynthetically active radiation (IPAR) relates directly to photosynthesis (Charles-Edwards, 1979) and to growth (Monteith 1981; Cannell, 1989). In Oregon, the estimated annual IPAR did not

Table 1. Characteristics of the study sites across the transect

Feature	Site						
	1	1A	2	3	4	5*	6
Site Name	Cascade head (Old-Growth)	Cascade Head (Alder)	Warings Woods	Scio	Santiam Pass	Metolius	Juniper
Physiographic Province <sup>1</sup>	Western coast range	Western coast range	Interior valley	Low-elevation west Cascades	High Cascades summit	Eastern high Cascades	High lava plain
Dominant species	<i>Picea sitchensis</i> , <i>Tsuga heterophylla</i>	<i>Alnus rubra</i>	<i>Pseudotsuga menziesii</i>	<i>Tsuga heterophylla</i> , <i>Pseudotsuga menziesii</i>	<i>Tsuga mertensiana</i>	<i>Pinus ponderosa</i>	<i>Juniperus occidentalis</i>
Elevation (m)	240	200	170	800	1460	1030	930
Slope (%)	12	0	13	12	0	0	0
Aspect	130°	—	160°	325°	—	—	—
Stem density (no.ha <sup>-1</sup> ) > 5 cm	385	1793	226	870	1740	600	141
Basal area (m <sup>2</sup> ha <sup>-1</sup> )	98.2	35	51.3	67	83.3	6.8	9.3
Percent IPAR	96.4	93.7	94.1	99.5	61.4	28.6	22.0

<sup>1</sup>Physiographic provinces from Franklin and Dyrness (1973).

Table 2. Minimum monthly predawn water potentials (MPa) for sites along the Oregon Transect, 1990–1991

Month	Site					
	1	2	3	4	5	6
May	—	-0.55	-0.55	—	-0.53	-1.08
June	-0.37	-0.75	-0.55	-0.58	-0.53	-0.95
July	—	-1.08	—	-0.72	-0.72	-2.20
Aug.	—	-1.76	—	-0.61	-0.76	-2.20
Sept.	—	-1.70	-0.65	—	-1.53	—
Oct.	-0.70	-1.96	-0.65	-0.69	-1.82	-2.50

relate well to growth (Fig. 2). From previous research, we recognize that much of the radiation intercepted during drought, frost, or high humidity deficits cannot be utilized due to stomatal closure. To take these physiological constraints into account, we developed some simple algorithms to calculate the amount of intercepted radiation actually utilized each day (Table 3). We have purposely defined broad thresholds and responses as these are more likely to apply to the wide range of species found across Oregon and can be derived from standard weather data (Running, Nemani & Hungerford, 1987).

The difference between IPAR and Utilized PAR represents the restrictions that climatic variables place on photosynthesis throughout the year. In our study, the climatic constraints ranged from less than 10% for the coastal rainforest to >75% where juniper (*Juniperus occi-*

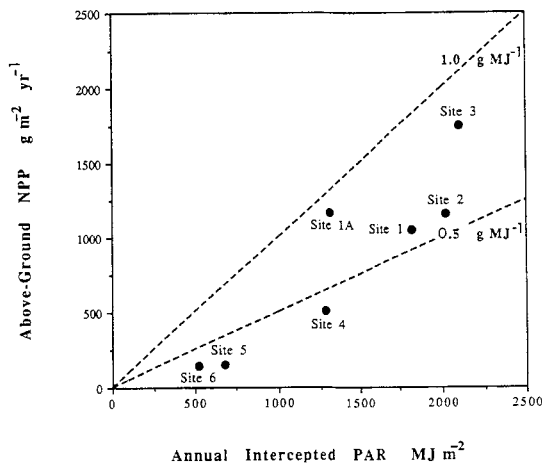


Fig. 2. Estimates of aboveground net primary production from annual intercepted PAR. Dashed lines express production rates (g of dry matter accumulated per MJ of PAR intercepted). Linear  $r^2 = 0.84$ .

Table 3. Criteria for reducing intercepted PAR, based on physiological thresholds applicable to all major tree species in Oregon

Freezing temperatures

● If less than  $-2^{\circ}\text{C}$ , assume no radiation utilized for 24-hour period

Soil drought

● If predawn water potential less than  $-1.5$  MPa, assume no radiation utilized

● If predawn water potential is between  $-1.0$  to  $-1.5$  MPa, assume half radiation utilized

Vapour pressure deficits (VPD)

● If VPD exceeds 25 mb, assume no radiation utilized

● If VPD is between 15 to 25 mb, assume half radiation utilized

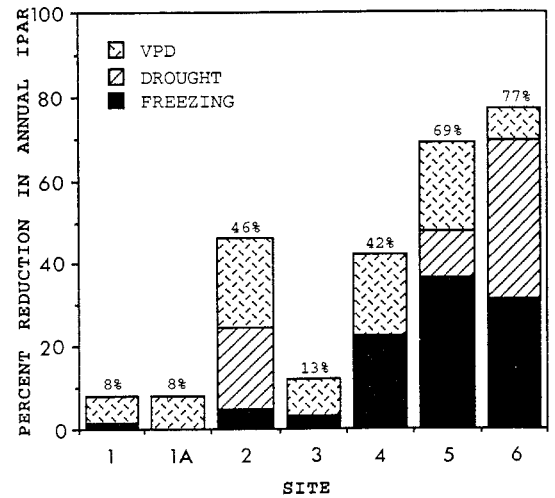


Fig. 3. The fraction of intercepted radiation not utilized by the various forests is shown as a function of freezing temperatures, drought, and excessive vapor pressure deficits (VPD). The total reduction in IPAR that could be utilized ranged from less than 10% at the coastal hemlock forest (Site 1) to 77% at the juniper woodland (Site 6). After Runyon (unpublished).

*dentalis* Hook) occurs (Fig. 3). Utilized PAR correlated closely with measured aboveground net primary production (NPP), with an aboveground efficiency of  $1.0$  g of biomass  $\text{MJ}^{-1}$  (Fig. 4). Only one plot, an old-growth Sitka spruce (*Picea sitchensis* (Bong.) Carr./Western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) forest, showed demonstrably less growth than predicted. Although old-growth forests are rare today, they are important because they bear witness to historical changes in climate and may be more susceptible to future changes than younger forests. Their physiology is different from younger forests in at least two important

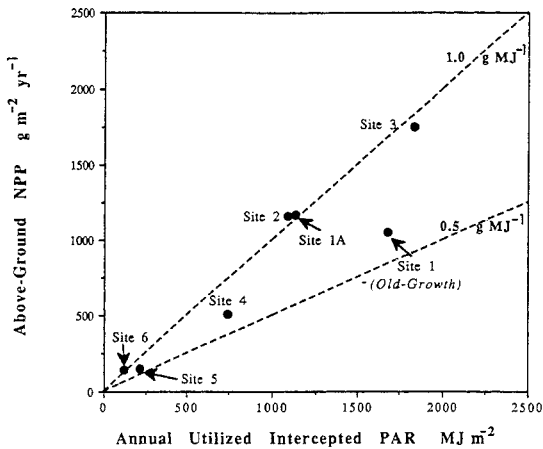


Fig. 4. Estimated aboveground Net Primary Production (NPP) compared to utilized PAR. This explains 98% of the variance in NPP for the range of forest stands across the Oregon transect. The old-growth stand was excluded from the regression. It effectively utilized 30% less PAR than indicated. Deducting an additional 100 MJ m<sup>-2</sup> for increased maintenance respiration compared to an adjacent 120-year-old stand brings the calculated NPP in line with that observed. After Ryan (unpublished).

ways. First, they maintain old branches that have progressively less ability to conduct water efficiently as they grow in length (Tyree & Sperry, 1988). Secondly, they have more living cells in their biomass than younger forests. These extra cells require carbohydrates for maintenance that could otherwise go toward growth (Ryan, 1990).

In old-growth Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), Lodgepole pine (*Pinus contorta* Dougl. ex Loud.), and Ponderosa pine (*Pinus ponderosa* Dougl. ex Loud.) forests it has been estimated that stomatal conductance and photosynthesis are reduced about 30% below that observed in forests where trees still grow in height (Kline, Reed, Waring & Stewart, 1976; Ryan, 1991; Yoder, 1992). The additional increase in maintenance respiration associated with increasing biomass was estimated using formulas outlined by Ryan (1990) that take into account sapwood volume, appropriately weighed mean annual temperature and maintenance respiration rates measured on western hemlock trees in Oregon (Ryan, unpublished). Maintenance respiration by the old-growth forest at site 1 was estimated at 230 g C m<sup>-2</sup> yr<sup>-1</sup>, only 60 g C m<sup>-2</sup> yr<sup>-1</sup> more than in an adjacent 120-year-old stand (Ryan, unpublished). Assuming dry matter contains 50%

carbon, this translates into about 100 g C m<sup>-2</sup> yr<sup>-1</sup> of biomass, taking into account the respiration cost of growth.

Reduced photosynthesis by old-growth forests, not maintenance respiration, appeared to be the major constraint on growth. We calculated the NPP of the old-growth stand, assuming first a 30% reduction in utilized PAR (1 640 MJ m<sup>-2</sup> reduced to 1 150 MJ m<sup>-2</sup>). We further reduced this estimate by 100 MJ m<sup>-2</sup> to account for the increase in maintenance respiration. With a conversion efficiency of 1.0 g MJ<sup>-1</sup>, the predicted and measured NPP were essentially the same (1 050 g m<sup>-2</sup> yr<sup>-1</sup> compared to 1 030 g m<sup>-2</sup> yr<sup>-1</sup> as noted in Table 1).

## Selecting remote sensing techniques to predict photosynthesis and growth

The above empirical analysis of the OTTER field measurements suggests that a relatively robust estimate of aboveground primary production may be evaluated from a limited number of canopy and environmental variables. These include:

1. incident PAR radiation
2. fraction of PAR intercepted by the canopy
3. air temperature
4. atmospheric vapor pressure deficit
5. environmental drought, as defined by pre-dawn leaf water potential
6. presence of "old-growth" stands.

Remotely sensed measurements of reflected solar and emitted terrestrial radiation have the potential for fulfilling these measurement requirements (Goward, 1989). In the Oregon transect study we collected remotely sensed measurements which address these biophysical variables. The measurements include standardized laboratory and field studies, aircraft-based observations and satellite data. These data have been compiled in a computer Pilot Land Data Base at NASA Ames Research Center. Data processing and analysis are now underway.

The principles for derivation of these biophysical measurements from remotely sensed observations have developed over the last quarter century. In general, the measured spectral radiant fluxes are diagnostic of surface and atmos-

pheric phenomena because the molecular composition of terrestrial materials alters the spectral radiant flux through selective absorption and scattering. The magnitude of the observed alteration is diagnostic of the presence and magnitude of the terrestrial phenomenon.

### Incident PAR solar radiation

The maximum daily insolation possible at any given location can be calculated from earth-sun relations. However, the solar radiation which reaches the biosphere is attenuated by cloud reflectance, scattering by molecules and aerosols and absorption by water vapor, carbon dioxide and ozone. Estimates of these atmospheric reductions in incident solar radiation may be derived from a number of satellite sensors. The most precise estimates may be acquired from geostationary orbits, where sensors “stare” at the earth. From these satellites, half-hourly updates of atmospheric conditions are possible (Tarpley, 1979). However, the data handling and processing demands with this approach are exceptionally large. A simpler approach is to use a one-time-per-day observatory in a sun-synchronous, polar orbit (Pinker, 1990). One of the most novel approaches developed to date to estimate the incident PAR flux uses noon-time ultraviolet measurements from the Total Ozone Mapping Spectrometer (TOMS; Eck & Dye, 1991). When daily estimates of radiation from the TOMS satellite are integrated for each month, good agreement with ground measurements results (Fig. 5).

### Canopy-intercepted PAR

Combinations of visible and near-infrared spectral reflectance from the earth are related to fractional capacity of vegetation canopies to absorb PAR radiation (Kumar & Monteith, 1981; Asrar, Fuchs, Kanemasu & Hatfield, 1984; Sellers, 1985; Gallo, Daughtry & Bauer, 1985; Goward & Huemmrich, 1992). One such combination is the normalized difference vegetation index (NDVI), which is the difference of these spectral measurements divided by their sum. Laboratory studies conducted on Douglas-fir canopies demonstrated that both chlorophyll concentrations and leaf structure affect this NDVI signal (Yoder, 1992). As a result, photo-

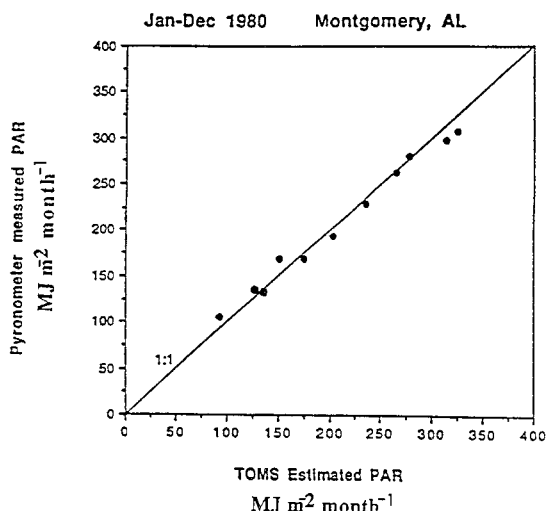


Fig. 5. Daily satellite measurements of cloud cover determined by ultra-violet reflectance allows monthly estimates of incident PAR radiation to match those measured at ground stations;  $r^2=0.98$ . (Eck & Dye, 1991).

synthesis, measured under near optimal conditions, was closely correlated to NDVI values (Hatfield, Asrar & Kanemasu, 1984; Yoder, 1992). In the field we found a good relationship between NDVI determined at 300 m above each stand and intercepted PAR measured beneath (Fig. 6). Differences in chlorophyll concentrations which exist in foliage across the transect have not yet been examined relative to the remotely sensed measurements (P. Matson and

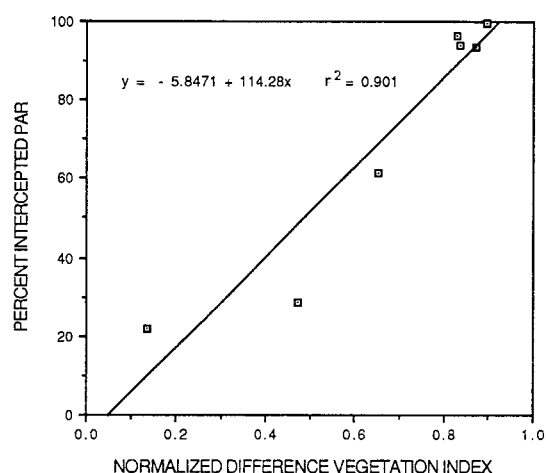


Fig. 6. The normalized difference vegetation index (NDVI) determined from 300 m altitude related closely to IPAR measured beneath the forest canopy (McCreight & Runyon, unpublished).

C. Billow, unpublished data from NASA Ames Research Center, Moffet Field, CA).

Derivation of these spectral measurements from spacecraft is also possible, at least at intervals between 10 days and a month (Goward, Markham, Dye, Dulaney & Yang, 1991). Fortunately, these periodic measurements provide an estimate of fractional PAR absorptance that is robust through overcast periods, which allows for interpolation of photosynthetic activity between successive measurements (Goward & Huemmrich, 1992). For the Oregon study NOAA satellite data, when corrected for variation in atmospheric clarity, provided regular updates to NDVI patterns across the entire transect (Spanner, unpublished, NASA Ames Research Center, Moffet Field, CA). These observations in general agree well with the aircraft and ground measurements with the exception of the winter period where deviations of uncertain origin are observed.

### **Air temperature, drought and vapor pressure deficit**

In logical order, those days with temperatures below freezing, with evidence of drought, and (or) extreme humidity deficits will reduce the IPAR utilized (Table 3). Temperature is a critical variable in calculating all three of these constraining factors and is important for its control on other ecosystem processes as well.

Measurement of terrestrial thermal infrared (TIR) emissions provide an estimate of the surface temperature. For non-desert regions of the earth the emissivity factor in Planck's equation is approximately 0.98. Atmospheric attenuation, predominately resulting from water vapor absorptance, may be reasonably addressed using two or more spectral measurements in the 8–14  $\mu\text{m}$  region (Price, 1984). It is therefore possible to estimate surface kinetic temperatures from spectral TIR observations. Such observations are acquired by the NASA TIMS (Thermal Infrared Multispectral Scanner) aircraft instrument and the satellite-based NOAA Advanced Very High Resolution Radiometer (AVHRR).

The thermal IR signal can be used to estimate air temperature because closed-canopy forests are within a few degrees of ambient air temperatures (Luvall & Holbo, 1989). A combination

of the NDVI from the visible and near-infrared measurements and the TIR measurements permits assessment of closed-canopy conditions and the temperature estimated for this condition typically is within 2°C of air temperature with an  $r^2 > 0.95$  (McCraith, unpublished).

Drought stops transpiration. A rise in leaf temperature above that of ambient air occurs, and is associated with a drying and warming of background litter and soils (Aston & van Bavel, 1972). The drying is closely correlated with increasing drought stress, as measured by predawn water potential (Fogel & Cromack, 1977). We can interpret drought-induced temperature responses in a scene if a range in vegetation density is present (Goward & Hope, 1989; Nemani & Running 1989; Price, 1990). Along the transect, those sites where drought occurred (Table 2) were characterized by large differences in the surface temperature over a range in NDVI values (Fig. 7). Under conditions where soil water was not limiting, the complex of ecosystems showed less than a 5°C difference in surface temperature, across the same range of NDVI measurements.

The atmospheric humidity deficit, expressed as vapor pressure deficit, affects stomatal aperture, even when soil water is not limiting. To estimate the vapor pressure deficit of the air requires, in addition to ambient temperature estimates, some measure of the water vapor content. Water vapor is the primary attenuator of TIR radiance but its impact is wavelength-dependent. It is therefore possible to estimate the amount of water vapor in the atmospheric column between the sensor and the ground by collecting dual-band spectral TIR observations (Justice, Eck, Tanre & Holben, 1991). Because the majority of water vapor in the column is near the surface an estimate of surface vapor pressure deficit can be computed with this measurement and the estimated ambient air temperature (Fig. 8).

### **Old-growth forests**

Standing biomass is important in estimating maintenance respiration. An accurate estimate of height is desirable to recognize when growth has stopped, and photosynthetic rates, defined in our model as a 30% reduction in utilized PAR, are applied. Conventional stereo images

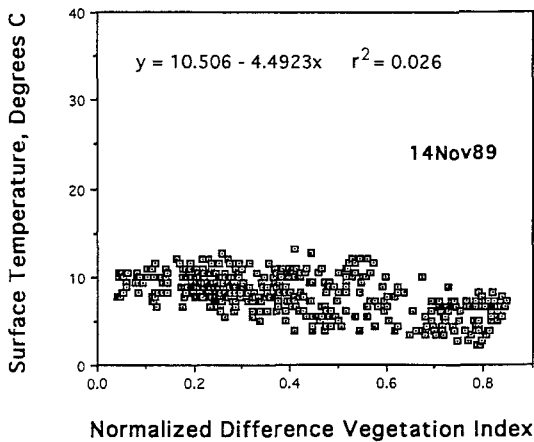
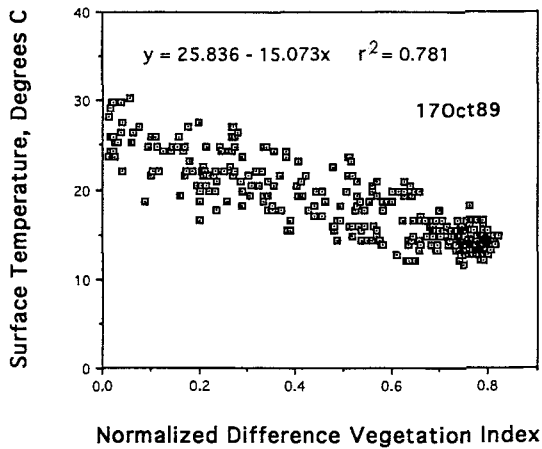


Fig. 7. Remotely sensed evidence of seasonal drought. Slope of surface temperature/NDVI steepens with drought. Near site 2, the end of the dry period in October revealed surface temperature variations in excess of 20°C, indicative of extreme drought stress on all vegetation (Goward, McCreight & Waring, unpublished).

are useful for estimating tree heights and standing biomass but images from satellites generally cover too much area in a scene to provide the desired resolution for estimating canopy height. As an alternative, variation in near-infrared and short-wave-infrared reflectance have been used in the Pacific Northwest region to distinguish old-growth forests from mature, and other age classes (Cohen & Spies, 1992). The local variation observed in temperature over a scene during the day may also provide an indirect measure of forest structure (Luvall & Holbo, 1989). Tree size can also be assessed by analyzing spectral differences in shadow observed at

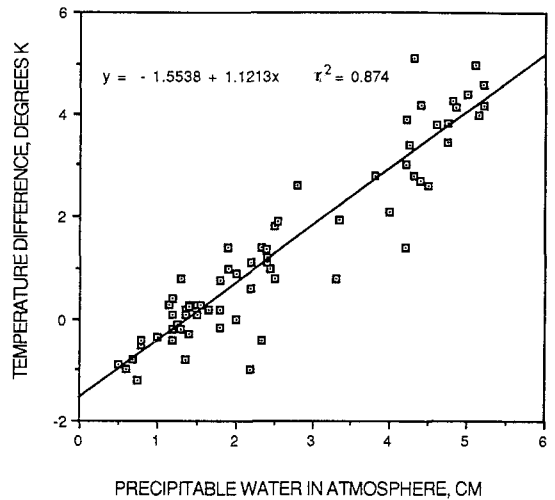


Fig. 8. Estimation of atmospheric water vapor content from two spectral wave lengths of thermal infrared radiance (after Justice et al., 1991).

varying sun angles (Li & Strahler, 1985; Franklin & Hiernaux, 1991).

In summary, currently available satellite-borne sensors offer the potential to obtain key biophysical measurements with which to characterize photosynthetic activity in the biosphere. Combinations of spectral observations from the ultraviolet, visible, near-infrared, shortwave infrared and thermal infrared provide critical information on energy availability in conjunction with physiological and environmental constraints which determine current rates of photosynthetic activity. The great advantage of satellite observations is that they provide consistent global coverage and fine spatial resolutions. The most serious current limitation is that most of these satellites provide only periodic measurements at intervals between 10 days and a month. This level of temporal precision may miss some critical events needed to monitor biospheric photosynthetic activity accurately. Within the Oregon Transect study we are now working toward a test of this methodology which will provide at least one critical evaluation of this approach.

## Conclusions

Research being carried out under the NASA OTTER project is exploring the potential for



monitoring biospheric activity with satellite-based remote sensing observations. A generalized model of biospheric activity is being investigated which considers photosynthetic activity as a balance between intercepted solar radiation and factors which limit the capacity of vegetation to utilize this energy. Results from field measurements indicate that the effects of air temperature, drought and atmospheric vapor pressure deficit explain much of the variance in rates of aboveground production per unit inter-

cepted PAR radiation. The effects of stand age and nutrient status are also being considered. Remotely sensed measurement procedures to consider each of these environmental and physiological factors are under investigation. Preliminary results indicate that these methods provide the needed information to characterize biospheric activity across the Oregon Transect. Generalization to global scales will depend on successful execution of similar studies in other biospheric regions of the globe.

## References

- Asrar, G., Fuchs, M., Kanemasu, E.T. & Hatfield, J.L. 1984. Estimating absorbed photosynthetic radiation and leaf area index from spectral reflectance in wheat. *Agronomy Journal* 76, 300–314.
- Aston, A.R. & van Bavel, C.H.M. 1972. Soil surface water depletion and leaf temperature. *Agronomy Journal* 64, 368–373.
- Cannell, M.G.R. 1989. Physiological basis of wood production: a review. *Scandinavian Journal of Forest Research* 4, 459–490.
- Charles-Edwards, D.A. 1979. Photosynthesis and crop growth. In *Photosynthesis and plant development* (ed. R. Marcelle, H. Clijsters & M. van Pouke), 111–124. The Hague: Junk.
- Eck, T. & Dye, D. 1991. Satellite estimation of photosynthetically active radiation at the Earth's surface. *Remote Sensing of Environment* 38, 135–146.
- Cohen, W.B. & Spies, T.A. 1992. Estimating structural attributes of Douglas-fir/western hemlock forest stands from LANDSAT and SPOT imagery. *Remote Sensing of Environment* 41, 1–18.
- Emmingham, W.H. & Waring, R.H. 1977. An index of photosynthesis for comparing sites in western Oregon. *Canadian Journal of Forest Research* 7, 165–174.
- Fogel, R. & Cromack Jr., K. 1977. Effect of habitat and substrate quality on Douglas-fir litter decomposition in western Oregon. *Canadian Journal of Botany* 55, 1632–1640.
- Franklin, J. & Hiernaux, P.H.Y. 1991. Estimating foliage and woody biomass in Sahelian and Sudanian woodlands using a remote sensing model. *International Journal of Remote Sensing* 12, 1387–1404.
- Franklin, J.F. & Dyrness, C.T. 1973. *Natural vegetation of Oregon and Washington*. Corvallis, Oregon, USA: Oregon State University Press.
- Gallo, K.P., Daughtry, C.S.T. & Bauer, M.E. 1985. Spectral estimation of absorbed photosynthetically active radiation in corn canopies. *Remote Sensing of Environment* 17, 221–232.
- Gholz, H.L. 1982. Environmental limits on above-ground net primary production, leaf area, and biomass in vegetation zones of the Pacific Northwest. *Ecology* 63, 461–481.
- Gholz, H.L., Grier, C.C., Campbell, A.G. & Brown, A.T. 1979. Equations for estimating biomass and leaf area of plants in the Pacific Northwest. *Forest Research Laboratory, Oregon State University, Corvallis, Oregon. Research Paper 41*.
- Goward, S.N. 1989. Satellite bioclimatology. *Journal of Climate* 7, 710–720.
- Goward, S.N. & Huemmrich, K.F. 1992. Vegetation canopy PAR absorptance and the normalized difference vegetation index: An assessment using the SAIL model. *Remote Sensing of Environment* 39, 119–140.
- Goward, S.N. & Hope, A.S. 1989. Evapotranspiration from combined reflected solar and emitted terrestrial radiation: Preliminary FIFE results from AVHRR data. *Advances in Space Research* 9, 239–249.
- Goward, S.N., Markham, B., Dye, D.G., Dulaney, W. & Yang, J. 1991. Normalized difference vegetation index measurements from the advanced very high resolution radiometer. *Remote Sensing of Environment* 35, 257–277.
- Hatfield, J.L., Asrar, G. & Kanemasu, E.T. 1984. Intercepted photosynthetic active radiation estimated by spectral reflectance. *Remote Sensing of Environment* 14, 65–75.
- Hunt Jr, E.R., Martin, F.C. & Running, S.W. 1991. Simulating the effects of climatic variation on stem carbon accumulation of a ponderosa pine stand: comparison with annual growth incremental data. *Tree Physiology* 9, 161–171.
- Justice, C.O., Eck, T., Tanre, D. & Holben, B.N. 1991. Effect of water vapor on the normalized difference vegetation index derived for the Sahelian Region from NOAA AVHRR data. *International Journal of Remote Sensing* 12, 1165–1188.
- Kline, J.R., Reed, K.L., Waring, R.H. & Stewart, M.L. 1976. Field measurements of transpiration in Douglas-fir. *Journal of applied Ecology* 13, 273–283.
- Kumar, M. & Monteith, J.L. 1981. In *Remote sensing of crop growth. Plants in the Daylight Spectrum* (ed. H. Smith), 134–144. New York: Academic Press.
- Li, X. & Strahler, A.H. 1985. Geometric-optical modeling of a conifer forest canopy. *I.E.E.E. Transactions on Geoscience and Remote Sensing* 23, 703–721.
- Luvall, J.C. & Holbo, H.R. 1989. Measurements of short-term thermal responses of coniferous forest canopies using thermal scanner data. *Remote Sensing of Environment* 27, 1–10.
- Monteith, J.L. 1981. Climatic variation and the growth

- of crops. *Quarterly Journal of the Royal Meteorological Society* 107, 749–774.
- Nemani, R.R. & Running, S.W. 1989. Estimation of surface resistance to evapotranspiration from NDVI and thermal-IR AVHRR data. *Journal of Climate and Applied Meteorology* 28, 276–294.
- Pierce, L.L. & Running, S.W. 1988. Rapid estimation of coniferous forest leaf area using a portable integrating radiometer. *Ecology* 69, 1762–1767.
- Pinker, R.T. 1990. Satellites and our understanding of the surface energy balance. *Palaeogeography, Palaeoclimatology, Palaeoecology* 82, 321–342.
- Price, J.C. 1984. Land surface temperature measurements from the split window channels of the NOAA 7 advanced very high resolution radiometer. *Journal of Geophysical Research* 89 D5, 7231–7237.
- Price, J.C. 1990. Using spatial context in satellite data to infer regional scale evapotranspiration. *IEEE Transactions on Geoscience and Remote Sensing* 28, 940–948.
- Running, S.W. 1976. Environmental control of leaf water conductance in conifers. *Canadian Journal of Forest Research* 6, 104–112.
- Running, S.W. & Coughlan, J.C. 1988. A general model of forest ecosystem processes for regional applications. I. Hydrologic balance, canopy gas exchange and primary production processes. *Ecological Modelling* 42, 125–154.
- Running, S.W., Nemani, R.R. & Hungerford, R.D. 1987. Extrapolation of synoptic meteorological data in mountainous terrain, and its use for simulating forest evapotranspiration. *Canadian Journal of Forest Research* 17, 472–483.
- Ryan, M.G. 1990. Growth and maintenance respiration in stems of *Pinus contorta* and *Picea engelmanni*. *Canadian Journal of Forest Research* 20, 48–57.
- Ryan, M.G. 1991. A simple method for estimating gross carbon budgets for vegetation in forest ecosystems. *Tree Physiology* 9, 255–266.
- Sellers, P.J. 1985. Canopy reflectance, photosynthesis, and transpiration. *International Journal of Remote Sensing* 6, 1335–1372.
- Tarpley, J.D. 1979. Estimating incident solar radiation at the surface from geostationary satellite data. *Journal of Applied Meteorology* 18, 1172–1181.
- Tyree, M.T. & Sperry, J.S. 1988. Do woody plants operate near the point of catastrophic xylem dysfunction caused by dynamic water stress? *Plant Physiology* 88, 574–580.
- Waring, R.H. & Franklin, J.F. 1979. Evergreen coniferous forests of the Pacific Northwest. *Science* 204, 1380–1386.
- Yoder, B.J. 1992. *Photosynthesis of conifers: influential factors and potential for remote sensing*. Ph.D. thesis, Oregon State University, Corvallis, OR.

## Acknowledgements

Many scientists involved in the Oregon Transect Ecosystem Project shared unpublished findings to permit this synthesis. To all we are grateful. Jeanne Panek and Beverly Law made helpful suggestions on earlier drafts of the manuscript. David Peterson, Branch Chief at NASA Ames Research Center, deserves special recognition for initiating the project. Support from Maurice Averner, Diane Wickland and Anthony Janetos at NASA Headquarters was essential, as was coordination of the NASA research planes under the direction of James Huning. Work supported here was under NASA grant NAGW-1717.