AN ABSTRACT OF THE THESIS OF

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Title: Photosynthesis of Conifers: Influential Factors and Potentials for Remote Sensing

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Remote sensing offers the potential for monitoring photosynthesis over large temporal and spatial scales. The purpose of this thesis is to provide information that will help to develop methods to predict photosynthesis from the light reflected by canopies.

The studies focused on a simple model of canopy photosynthetic potential: $A_{canopy} = \epsilon \cdot APAR$, where A_{canopy} is photosynthetic potential, APAR is the fraction of incident visible light that can be absorbed by the canopy, and ϵ is the light use efficiency. The first experiment showed that for small canopies of Douglas-fir seedlings, ϵ was not a constant, even though environmental conditions were the same for all measurements of photosynthesis. APAR alone explained 36% of the variability in canopy photosynthesis. Photosynthetic capacity of needles from the top of a canopy was a good indicator of ϵ: A model combining APAR and photosynthetic capacity explained 83% of the variation in canopy photosynthesis. Chlorophyll concentration

was positively correlated with photosynthetic capacity, but had no measurable correlation with APAR. Leaf area alone explained most of the variation in APAR (R^2 = 0.87).

The second study demonstrated that the normalized difference vegetation index (NDVI), derived from amounts of red and near infrared light reflected by a vegetation, was a better indicator of $\epsilon \cdot$ APAR than of APAR alone. This was because changes in leaf area at constant chlorophyll concentration caused reflectance to change in the near infrared but not the visible region. NDVI, however, was sensitive to both near infrared and visible reflectance. When chlorophyll varied at constant leaf area, NDVI varied but APAR did not. Because of the relationship between chlorophyll and photosynthetic capacity, and because variation in chlorophyll caused changes in the reflectance of red light, NDVI incorporated information about ϵ.

The third study demonstrated that in a mature hemlock stand, photosynthetic capacity did not change through the course of a year, despite below-freezing temperatures on two sampling dates, or in response to increased leaf nitrogen after fertilization. Previous studies have shown that many conifers have reduced photosynthetic capacity during the winter, and that photosynthetic capacity is often related to leaf nitrogen. This study points out exceptions that need to be considered in models of whole canopy photosynthesis.

Photosynthesis of Conifers:
Influential Factors and Potentials for Remote Sensing

by

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INTRODUCTION

In order to address problems of global change, ecological studies must focus on large scales of time and space. Tools are needed that measure or model photosynthesis and other processes on these large scales. Remote sensing offers promising potentials because airborne and spaceborne sensors cover large areas and because repetitive measurements by satellites give repeated measures through time. Field and modeling efforts have demonstrated that light reflectance patterns may be used to derive indices of canopy photosynthetic potential. However, most research to date does not consider the impact of varying leaf chemistry and photosynthetic capacity on both reflectance signals and canopy photosynthesis. The studies in this thesis are designed to help fill that information gap.

Direct measurement of canopy photosynthesis requires determination of CO_2 concentrations and fluxes above canopies. There has been some success with this type of measurement (Matson and Harris 1988), but currently it is not a viable approach for most systems. An alternative is to develop models that predict actual photosynthesis from measurable characteristics of the canopy and its environment. There are two important criteria for such a model: the required input must be measurable, and the model must provide predictions of acceptable accuracy.

Two general approaches are used to model photosynthesis at the canopy level. One approach integrates leaf-level processes through time and space (Agren *et al.* 1991 provide a recent review of process-level models). An advantage of process-level models is that they are based on well-studied, fundamental processes, and in theory they should yield very accurate predictions. A disadvantage is that most process-level models require detailed input variables that are difficult to obtain through remote

sensing. However, important advances are being made with at least one process model, FOREST-BCG, so that it can be driven by remotely sensed input (Running *et al.* 1989).

Another approach is to start with a simple model involving few terms, and to add complexity to the model only when it clearly enhances accuracy. I have taken this approach. Central to the studies in this thesis is the model:

$$A_{canopy} = \epsilon \cdot APAR \quad (1)$$

where A_{canopy} is canopy CO_2 assimilation, ϵ is a coefficient of conversion efficiency of visible light, and APAR is the amount of photosynthetically active radiation absorbed by the canopy. This model is derived from work by Monteith (1977) and others, who showed that net primary production by crop plants is directly proportional to the integrated APAR over a growing season.

Both ϵ and APAR are functions of plant properties and environmental conditions. Running (1991) noted that ϵ incorporates meteorological and biochemical components. Biochemistry of leaves affects their photosynthetic capacity, whereas environmental conditions (e.g. temperature, water stress) at any point in time can limit actual photosynthesis below that potential. Likewise the total light absorbed at any point in time is determined by the amount of light striking the canopy and the potential of the canopy to absorb light.

The studies in this thesis were concerned *only* with the plant properties that determine ϵ and APAR. Their product can be considered the photosynthetic potential of the canopy, which sets an upper limit to total photosynthesis. A model of actual photosynthesis would require input of environmental variables that could reduce photosynthetic rates below the maximum potential. That is beyond the scope of this

study.

Each of the three chapters was written as a separate paper that stands alone. Each one deals with some aspect of equation 1, but each has independent objectives relevant to the specific study.

In Chapter 1 I analyzed equation 1 in a context that could be applicable to remote sensing. The questions I asked in this study include: Is ϵ a constant (in other words, is canopy photosynthesis a linear function of the amount of light absorbed)? If ϵ is a variable, can photosynthetic capacity at the top of the canopy explain a significant amount of that variability? Can chlorophyll concentration of leaves at the top of the canopy be used as an indicator of photosynthetic capacity? Is the ability to absorb light solely a function of leaf area and display, or do variations in leaf chlorophyll cause significant variation in APAR? The emphasis was on conditions at the top of the canopy because this is the region that a sensor can detect. Likewise, I chose chlorophyll as a potential indicator of photosynthetic capacity because changes in chlorophyll concentration should be detectable through changes in reflectance of visible light.

In Chapter 2 my goal was to evaluate methods for remotely sensing the photosynthetic potential of a canopy. The emphasis was on vegetation indices derived from reflectance of red (R) and near-infrared (NIR) light. Many studies have shown that indices such as the simple ratio (R/NIR) and the normalized difference vegetation index (NIR-R/NIR+R) may be related to structural properties of canopies, including leaf area, total biomass, or APAR. I tested the hypothesis that these indices are better indicators of canopy physiology than of canopy structural features.

The experiments for Chapters 1 and 2 were conducted in a laboratory on very small canopies. I chose this experimental approach for three reasons. First, it allowed me to induce independent variation in leaf area and photosynthetic capacity. In

field studies these variables are often autocorrelated. Second, it was possible to measure net CO_2 assimilation directly with these small canopies. Direct measurements of CO_2 uptake by whole canopies are difficult in the field. Third, accurate measurements of canopy reflectance were possible without interference due to changing sun angle, clouds, variable background, or other unknowns. These advantages allowed me to analyze the independent effects of particular canopy features on reflectance spectra. The drawback to a laboratory study is that conditions are artificial. For example, Chapter 1 demonstrates that variation in photosynthetic capacity at the leaf level can effect variation in whole canopy photosynthesis. Field studies are needed to clarify how variable photosynthetic capacity is in natural systems, and to what extent APAR and photosynthetic capacity tend to be correlated.

Chapter 3 deals with the variability of leaf-level photosynthetic capacity in a natural forest of western hemlock. Specifically, I investigated the effects of fertilization on photosynthetic capacity and determined whether the capacity changed through an annual cycle. Many other studies on conifers have shown that nitrogen fertilization enhances photosynthetic capacity and freezing winter temperatures can cause a depression. However, this hemlock stand provided a good opportunity to test the universality of these relationships. This is because light limitations in the very dense stand might be expected to temper the effects of nitrogen. Also, western hemlock does not grow in areas of severe winter cold, so it might not undergo the same dormancy and associated decline in photosynthetic capacity that many other conifers experience.

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Chapter I

EFFECTS OF LIGHT ABSORPTION AND PHOTOSYNTHETIC CAPACITY ON PHOTOSYNTHETIC POTENTIAL OF WHOLE CANOPIES

ABSTRACT

The upper limit to canopy photosynthesis, or canopy photosynthetic potential, should be the product of light absorption potential and the biochemical efficiency of energy conversion. I tested the hypothesis that this model could be used to predict photosynthetic potential when leaf-level photosynthetic capacity from the top of the canopy is used as an indicator of biochemical efficiency. Douglas-fir seedlings were grown under a variety of shade and fertilization treatments to induce variation in photosynthetic capacity. Canopy photosynthetic potential was measured in large gas exchange chambers, and photosynthetic capacity of foliage was measured on excised twigs from the top of the canopy.

Light absorbance (400-700 nm) by the canopies was related to leaf area index by a simple Beer's Law exponential function. Variations in leaf chlorophyll had no measureable impact on light absorbance. Light absorbance alone explained only a third of the observed variation in canopy photosynthesis; however, light absorbance and photosynthetic capacity together explained three-quarters of the observed variation.

The concentration of chlorophyll was closely correlated with the photosynthetic capacity of foliage that had been grown in full sun ($R^2=0.80$), and chlorophyll was better than nitrogen at predicting photosynthetic capacity of shaded foliage. These findings suggest that the photosynthetic potential of canopies might be derived by some biophysical reflectance measures of chlorophyll concentration and light absorption potential, the subject of the next chapter.

INTRODUCTION

In order to address problems of global change, ecological studies must focus on large scales of time and space. Remote sensing is a promising tool for evaluating ecosystem processes such as photosynthesis at large scales, and methods are needed that allow measurement or modelling of photosynthesis from remotely sensed data. With current technology it is not possible to make direct measurements of CO_2 flux using remote sensors. Another approach is to predict photosynthesis indirectly from remote estimates of the photosynthetic potential of a canopy along with environmental constraints that may limit actual photosynthesis below the maximum potential. The purpose of this study is to analyze a simple model of photosynthetic potential that is amenable to remote sensing:

$$(1) \qquad A_{canopy} = \epsilon \cdot \text{APAR}$$

where A_{canopy} is potential canopy CO_2 assimilation, ϵ is a coefficient of the biological potential for energy-conversion efficiency, and APAR is the fraction of incident photosynthetically active radiation (PAR) that can be absorbed by the canopy.

Environmental conditions may constrain both ϵ and APAR. Total light absorption, for example, depends on the biological properties of leaf area, leaf arrangement, and leaf optical properties and on the environmental properties of sun angle, solar intensity and atmospheric conditions. This study was restricted to an analysis of the biological elements that determine ϵ and APAR. Together they set an upper limit to A_{canopy}, or the canopy photosynthetic potential.

The purpose of this study was not to identify a perfect model of canopy photosynthesis. Excellent process-level models are now being developed for this purpose.

Instead, my goal was to evaluate the explanatory power of a very simple model, and to identify indicators for the terms in the model that could be sensed remotely. Specific objectives were to determine:

1. Is ϵ a constant?
2. If ϵ is a variable, can variablility of ϵ be explained by the photosynthetic capacity (per unit leaf) at the top of the canopy? If so, what measure of photosynthetic capacity is best?
3. Can the nitrogen and/or chlorophyll concentration of leaves be used as an indicator of their photosynthetic capacity, and therefore ϵ?
4. Is APAR solely a function of leaf area and display, or do variations in leaf pigmentation affect APAR as well?

An explanation and justification of these objectives is developed below.

BACKGROUND

Derivation of the Model

In the 1960's a number of studies demonstrated that the net primary production of many crop plants was proportional to the amount of photosynthetically active radiation absorbed by the plant canopy through time (Shibles and Weber 1965, Monteith 1966, Puckridge and Donald 1967):

$$\text{NPP} = \epsilon' \cdot \text{APAR} \qquad (2)$$

In equation 2, ϵ' is a biomass conversion efficiency rather than a photosynthetic light

use efficiency, as in equation 1. Other researchers subsequently found similar relationships for other crop plants (e.g. Gallagher and Biscoe 1986, Green et al. 1985, Kasim and Demet 1986) as well as forest trees (Linder 1985, Jarvis and Leverenz 1983, Cannell *et al.* 1987, Russell *et al.* 1989).

Implicit in this simple, empirical relationship is the corollary that instantaneous light absorbance by the canopy should be related to changes in instantaneous photosynthesis, as expressed in equation 1.

Determinants of ϵ

The efficiency terms in equations 1 and 2 are different. Determinants of photosynthetic light use efficiency (ϵ) are a subset of determinants of biomass conversion efficiency (ϵ') because net photosynthesis is only one of many factors affecting total growth. Several studies have shown that ϵ' is surprisingly conservative, especially for healthy C_3 crop plants (e.g. Monteith 1977, Monteith and Elston 1983). As discussed above, net growth of crop plants is often directly proportional to integrated APAR, implying ϵ' is a constant. If ϵ' is constant, ϵ probably is also. The constancy of ϵ' in many studies is probably because the plants studied are fertilized and irrigated crops that are near the maximum ϵ' possible for the species. Objective 1 of my study was to test the null hypothesis that ϵ is constant (i.e. APAR is directly proportional to A_{canopy}) when plants of the same species have different nutritional histories.

The photosynthetic light use efficiency of a canopy, in the restricted sense defined above, is directly related to the biochemical capacity of the canopy to fix CO_2 (Field 1991, Running 1991). If canopy biochemistry varies, ϵ should vary. It should be possible to predict ϵ from canopy biochemistry; the problem is to determine a good predictor. For the purposes of this study, the predictor needed to be detectable

through remote sensing. The first step was to determine whether photosynthetic capacity of individual leaves at the top of the canopy could be used to predict whole-canopy photosynthetic potential (Objective 2). The reason for restricting the analysis to the canopy top is that this region has the most influence on canopy reflectance properties, especially of visible light. The second step was to determine whether photosynthetic capacity of foliage can be predicted from a property of leaves that may be sensed remotely (Objective 3).

Photosynthetic capacity of single leaves has been studied intensively, but there is limited information on how photosynthetic capacity of individual leaves relates to the capacity of whole canopies. Light-saturated photosynthetic capacity of individual leaves varies greatly with canopy depth (Jarvis, James and Landsberg 1976, Leverenz and Jarvis 1979, Hollinger 1989). Photosynthesis of whole canopies is rarely light saturated anyway (if it were, whole-canopy photosynthesis would not increase linearly with APAR), so a light-saturated photosynthetic capacity would seem a poor indicator of the biochemical fixation capability of the canopy. However, in theory photosynthetic capacity through a canopy profile should decline as a predictable function of the light environment (Takenaka 1989, Farquhar 1989, Field 1991), and studies of nitrogen profiles through canopies appear to support this idea (Field 1983, Hirose and Werger 1987, Hollinger 1989). Thus it is reasonable to expect that photosynthetic capacity at the top of a canopy might be a good predictor of ϵ.

There have been reports that both nitrogen (Card *et al.* 1988, Wessman *et al.* 1988) and chlorophyll (Curran and Milton 1983, Feng and Miller 1991) concentrations are detectable through remote sensing, although it is easier to quantify chlorophyll through remote sensing because it is the dominant factor affecting the reflectance of visible light from vegetation. Nitrogen concentration is known to be a good predictor of photosynthetic capacity at the leaf level across a broad array of plant life

forms (Field and Mooney 1984), although the relationship appears to be weaker for evergreen sclerophylls (Field and Mooney 1984), especially if leaves have developed under light limiting conditions (Rose 1990, Chapter 3). Canopy nitrogen content has been tightly linked to above-ground productivity (Vitousek 1982).

Chlorophyll is generally not as closely correlated with photosynthetic capacity (Bjorkman 1981), but chlorophyll and nitrogen are often related. Linder (1980) found that when Scots pine are grown in controlled environmental conditions, chlorophyll concentration can be used as a reasonable indicator of nitrogen concentration. Relationships between chlorphyll content per unit ground area and crop productivity have also been demonstrated (Oquist *et al.* 1982).

Chlorophyll and nitrogen both have advantages and disadvantages as potential indicators of ϵ. Chlorophyll is more amenable to remote sensing, and nitrogen is usually more closely linked with photosynthetic capacity. I considered both of them (Objective 3).

Determinants of APAR

Essentially all of the visible light striking a canopy is absorbed (APAR), reflected (PAR_{refl}), or transmitted through the canopy (PAR_{trans}) (a very small amount is absorbed and then dissipated through fluorescence). PAR_{refl}, or canopy albedo, is small and relatively constant for conifers canopies (10-15%, Jarvis 1979), so APAR (as a proportion of incident light) is nearly proportional 100%-PAR_{trans}.

Light transmission through plant canopies is often modelled with a simple analog of Beer's Law (equation 3, below), where k is an extinction coefficient that typically ranges between 0.3 and 0.6 for conifer canopies (Kira 1975, Jarvis *et al.* 1976) and LAI is the leaf area index (total leaf area per unit ground area). Chloro-

phyll concentration of leaves is not explicitly defined in this equation; k is generally described as a function of canopy geometry and leaf distribution (e.g. Norman and Jarvis 1975).

As explained above, chlorophyll concentration should be at least loosely related to photosynthetic capacity. The role of chlorophyll, of course, is to absorb light, so one would also expect a relationship between chlorophyll and APAR. It was important for this study to determine whether chlorophyll concentration was correlated with both ϵ and APAR. I analyzed the effect of chlorophyll concentration on PAR_{trans} (Objective 4) by evaluating how well models that include chlorophyll (equations 4, 5 and 6) improve explanation of PAR_{trans} variation over the Beer's Law model that is based only on LAI (equation 3):

(3) $$PAR_{trans} = e^{-k(LAI)}$$

(4) $$PAR_{trans} = e^{-k(Chl)(LAI)}$$

(5) $$PAR_{trans} = e^{-k1(LAI) + k2(Chl)}$$

(6) $$PAR_{trans} = e^{[k0 + -k1(LAI) + k2(Chl)]}$$

METHODS

Plant Material

The observational units for this study were 'miniature' canopies: assemblages of Douglas-fir seedlings grown in close proximity. There were several reasons for

this choice. First, I was able to place entire canopies into large chambers to measure gas exchange. Second, the small-sized unit permitted a reasonable replication. Finally, I was able to maintain this plant material in a greenhouse and manipulate the growth environment to induce variation in canopy structure and function. An implicit assumption in my methodology is that the miniature canopies mimic the behavior of mature tree canopies. Obviously there are differences. For example, the canopy architecture of a cluster of seedlings may be different from mature trees, and this could alter the relationship between leaf area and APAR. On the other hand, the miniature canopies permit a controlled test of my hypotheses not easily achieved under field conditions.

Each miniature canopy consisted of 20 seedlings growing individually in two-inch 'super-tubes' attached together by a holder in a four-tree by five-tree matrix. The seedlings were planted from 2-0 nursery stock in May, 1989. I placed the canopies on an outdoor nursery bed where they were maintained through the summer of 1989 with frequent watering and three applications of a half-strength commercial fertilizer. The canopy positions were rotated every two to three weeks to maintain fairly uniform growing conditions. In September, dead trees were removed from 24 of the planting blocks and replaced with vigorous trees from other blocks. I then moved these 24 canopies to a glasshouse and maintained them for three weeks with daily watering. Artificial lights provided 600 μmol m^{-2} s^{-1} PAR at the top of the canopies on a 16.5 hour photoperiod. Total light at midday with light cloudy skies was 800-900 μmol m^{-2} s^{-1} PAR. On September 30 the canopies were randomly assigned to shade and fertilization treatments, which were maintained for 14 weeks before physiological measurements were initiated.

Shade and Fertilization Treatments

I subjected canopies to shade and fertilization treatments to induce a range of canopy physical and chemical properties. Nitrogen was supplied to vary photosynthetic capacity and to create a range of nitrogen and chlorophyll concentrations in leaves. Different light levels were used to test more rigorously the relationships between canopy chemistry and photosynthesis, because shaded leaves typically have lower photosynthetic capacity and higher chlorophyll than sun-exposed leaves (Bjorkman 1981). I also used different levels of magnesium and iron in the fertilizer solutions in an attempt to uncouple nitrogen and chlorophyll, but these treaments had no effect. Leaf shedding occurred with some treatments, which produced canopies with varying leaf area.

The experimental treatments included three levels of nitrogen (0, 0.008 M and 0.040 M; applied as NH_4^+ and NO_3^- in a 1:2 ratio), two levels of Mg (0 and 0.002 M), and two levels of shading (shaded and unshaded) with two replications of each treatment. In addition to the prescribed nutrients, all trees were fertilized with a solution containing 0.004 M K^+ and 0.001 M Ca^{+2}, SO_4^{-2} and PO_4^{-2} plus micronutrients (Fe, 2 ppm; Cu, Zn and Mn, 0.3 ppm; B, 0.15 ppm; Mo 0.025 ppm).

The 20 trees in each canopy were grown in separate containers, so the nutrient solutions were applied to individuals. The application rate was 10 ml per tree, administered every four to six days. All trees were flushed with water before the nutrient solutions were added and at least once per day on all other days.

Forty percent shade cloth was placed entirely around two sets of twelve canopies (complete complements of the fertilization treatments) to create shade treatments. Because the artificial lights were not directly over the canopies, direct-beam light

passed through the shade cloth at an acute angle, so the actual light level at the top of the shaded canopies was less than 20% of unshaded canopies -- averaging 100 μmol m^{-2} s^{-1} in the absence of natural light, and increasing to 200-300 μmol m^{-2} s^{-1} PAR with natural light on a day with light clouds.

Although the trees in this experiment did not go through a chilling period, some of the fertilized trees flushed with new growth after ten weeks of treatment. The new growth was clipped off as soon as it appeared to avoid confounding problems of phenological differences in the analysis of canopy photosynthesis.

Photosynthetic Capacity

I evaluated three measures of photosynthetic capacity from curves relating CO_2 assimilation rate to different CO_2 concentrations in the cuvette and in the leaf mesophyll. One measure was A_{max}, the photosynthetic rate under 'optimum' conditions with saturating light and CO_2 in the bulk air around leaves at 350 μl l^{-1}. The value of A_{max} is a function of both stomatal conductance and biochemical capacity of the leaf mesophyll. The second was the assimilation rate when CO_2 concentration internal to the leaf (C_i) was 350 μl l^{-1} (A_{ci350}). This is the photosynthetic rate that should occur if stomatal conductance were infinite. Its value is primarily a function of the activity of the primary carboxylating enzyme, Rubisco (ribulose bisphosphate carboxylase oxygenase), and the ability of the electron transport system to recycle ribulose bisphosphate, the CO_2-accepting sugar (Farquhar *et al.* 1980). The third measure was the activity of Rubisco (designated $A_{rubisco}$) itself, determined from the initial slope of A/C_i curves (CO_2 assimilation *vs.* CO_2 concentration in the leaf mesophyll).

A/C_i curves were measured with a LiCor 6200 photosynthesis system (McDermitt *et al.* 1989) on a 5 to 8 cm segment of stem removed from the top middle

section of each canopy. The measurement procedure was similar to that described in Chapter 3, except that photosynthesis and stomatal conductance were logged continuously as CO_2 in the cuvette dropped from about 500 μl l^{-1} until net assimilation was less than 0.03 μmol m^{-2} s^{-1}. After gas exchange measurements, needles were removed from the twig and their projected area determined with a LiCor 3050A Leaf Area Meter. Cuvette temperature averaged 27° C during measurements, vapor pressure deficit averaged 1.3 kPa, and light at the leaf surface averaged 1800 μmol m^{-2} s^{-1}.

Because the measurement procedure required a very large difference between CO_2 concentration in the cuvette and in the ambient air, small leaks could cause significant errors in the calculation of the initial slope (McDermitt *et al.* 1989). I minimized leaks by inserting the cut end of the twig into a small water reservoir that could be entirely enclosed in the cuvette. I took further precautions by replacing the foam gaskets on the cuvette following every third or fourth measurement. Finally, I determined that the small remaining leaks could not be ignored with the closed system. I performed a leak test (LiCor 1990) between every second or third measurement. With these values I made mathematical corrections to photosynthesis, conductance, and C_i using procedures described by LiCor (1988).

The initial slopes of the A/C_i curves ($A_{rubisco}$) were evaluated by regression analysis of points through the linear portion of curves. Between 16 and 40 data points were used in each regression. All except one regression had an R^2 of 0.97 or greater. A_{ci350} and A_{max} were evaluated from analyses of graphs relating A to CO_2 concentrations in the leaf mesophyll and in the cuvette, respectively.

Measurement of Whole Canopy Photosynthesis

Whole canopy photosynthesis was measured in the Plant-Environment Research Chamber (PERCH) system at Oregon State University. Each chamber is a cylinder with 1.3 m^2 floor space and 1.5 m tall. Charcoal-filtered air is pushed through the chambers on a flow-through basis and stirred by a fan internal to each chamber. I measured the air flow rate through each chamber with a vane anemometer inserted into the exit pipe. Light was supplied by 1,000 watt metal halide lamps suspended over each chamber. This provided an average 480 μmol m^{-2} s^{-1} PAR at the tops of the canopies. The temperature of the chambers averaged 25 ^{o} C during measurements and was controlled by a heating/cooling system in the air supply manifold. Relative humidity of the inflowing air was maintained near 45% (vapor pressure deficit = 1.7 kPa) by a steam generator. Measurements were made between 10:00 PM and 5:00 AM because CO_2 concentration of inflowing air was more stable during those hours.

At the time of my measurements, the PERCH system was not developed to separate gas exchange of roots from shoots, so I measured net photosynthesis of entire canopies (including roots). I measured CO_2 exchange both in the light and the dark after 30 minutes equilibration time, and from the two measures I attempted to calculate total gross photosynthesis. However, additive measurement errors proved unacceptable, so the values reported are the net CO_2 uptake of entire canopies measured in the light.

I used a LiCor 6250 infrared gas analyzer to measure CO_2 concentrations at the inlet and outlet ports of the chambers. The LiCor 6250 was part of a LiCor 6200 photosynthesis system with an external flow valve, to which a length of tubing was attached. The photosynthesis system was set in 'flow-through' mode, and a connector

at the end of the tubing was attached to the chamber port. The LiCor pump was used to pull air in from the port, and readings of CO_2 concentration were logged every 10 s for one or two minutes, and the readings were averaged. The process was repeated several times on both inlet and outlet ports, and the CO_2 differential was calculated for each pair of inlet/outlet measurements. The final CO_2 differential for each measurement of photosynthesis was evaluated from the mean of the paired measurements. The net gas exchange was calculated from the change in CO_2 concentration divided by the air flow rate.

Measurements of APAR

Three measurements were used to calculate the percentage of photosynthetically active radiation that was absorbed by each canopy (APAR): Total light (PAR_{total}) with no canopy, transmitted light (PAR_{trans}) through the canopy, and reflected light (PAR_{refl}) from the canopy surface. APAR was calculated from the formula:

$$APAR\ (\%) = 100\% - PAR_{trans}(\%) - PAR_{refl}(\%)$$

PAR_{trans} was evaluated from the amount of light transmitted to the base of the canopies relative to the amount of light in the same location without the canopies, PAR_{total}. (This is a slightly different approach from the standard procedure of determining PAR_{total} at the top of a canopy, because under artificial lights the amount of light changes significantly when the source is a short distance away). PAR_{total} and PAR_{trans} were measured in the chambers used for measurements of photosynthesis. After the gas exchange measurement was completed, PAR was measured with a Decagon ceptometer, using only the photodiode at the tip, at 12 defined positions on the top of the planting block, beneath the seedlings. PAR_{trans} was calculated as the average of the twelve measurements, weighted by the number of trees around that

point. Then an empty planting block was placed in the identical position in the chamber, light measurements were made in the same positions, and PAR_{total} was calculated from these measurements. I used a similar approach to evaluate APAR of leaves only, except that in this case PAR_{trans} was measured under a canopy of live stems from which all leaves had been removed.

PAR_{refl} was measured separately. The canopies were placed under an integrating sphere light source, and per cent reflectance was measured relative to a barium sulfate plate with a Spectron SE-590 spectroradiometer (details are in Chapter 2). Per cent reflectance between 400 and 700 nm was averaged to determine PAR_{refl}.

Measurements of Leaf Area and Leaf Chemistry

Some of the experiments in Chapter 2 and one analysis in this chapter (APAR *vs.* leaf area) involved both whole canopies (20 seedlings) and half canopies (every other seedling removed). All of the samples for leaf area and leaf chemistry, described below, were taken separately from the trees that made up each 'half canopy'. Data from the two halves were averaged for the 'whole canopy' measurements.

Specific leaf area. At the time of measurement, all canopies had two or three age classes of needles. Preliminary measurements showed that the needles formed in the summer of 1989 (current needles) had significantly different specific leaf area (SLA; $cm^2\ g^{-1}$) compared with older needles, but the SLA of the two older age classes did not significantly differ. Two samples (approximately 5 cm^2) of needles of the current age class and one of the older age classes were removed at random from each half-canopy. Projected areas of each sample were measured with a LiCor 3050A leaf area meter, and the needles were dried for seven days at 70°C and weighed. For each age class, there was no significant difference among all canopies in the shaded treat-

ments and among all in the unshaded treatments, so the values of specific leaf area were pooled by age class and shading treatment.

Chlorophyll. Three samples of needles of approximately 1 cm^2 each were removed at random from each half-canopy and immediately placed in a cooler (approximately 5° C). Two of the samples were for the current age class, and one was for the older age class. Within two hours, the samples were removed one at a time from the cooler and the surface area determined with a LiCor 3050A leaf area meter. Samples were then placed in 4 ml dimethyl formamide and stored in the dark at 5°C for three days. Total chlorophyll was calculated after measuring absorbance of the resultant solution at 664.5 and 647 nm (Inskeep and Bloom 1985). The values of the two current age class samples were averaged for each half-canopy. The total chlorophyll content of each half-canopy was calculated from the product of chlorophyll concentration and total leaf area, by age class.

Total leaf area. At the end of the experiment all of the needles were removed from all of the 240 trees in the experiment and separated into current and older age classes and by half-canopies. These were dried to constant weight at 70° C and weighed. Total leaf area was determined from the product of the specific leaf area for each age class and the total leaf mass. The leaf area index (LAI) of each canopy was calculated by dividing the total leaf area by the projected area of the canopy.

Nitrogen. After the dried needles were weighed, a subsample (approximately 25% of the total) of each collection was ground in a Wiley mill. The ground leaf samples were analyzed for concentration of total nitrogen after Kjeldahl digest. The total nitrogen content of each half-canopy was determined from the product of nitrogen concentration and total leaf area, by age class.

Statistics

The independent variables in this experiment are canopy chemistry and leaf area, which varied continuously, not the light and fertilization treatments, which varied discreetly. Light and fertilization were applied only as a means to create a range of the independent variables. Regression analysis with SAS software (SAS 1985) was used to identify relationships among variables and test the goodness of fit of models.

RESULTS

Effects of Treatments

As expected, the shade and fertilization treatments created a broad range of nitrogen (8.0 to 30.0 mg dm^{-2}; 7.9 to 29.7 mg g^{-1}) and chlorophyll (2.6 to 6.9 mg dm^{-2}; 2.1 to 7.6 mg g^{-1}) concentrations as well as total leaf area (0.27 to 1.14 m^2; LAI=1.5 to 6.4). Variations in total leaf area and nitrogen concentration were generally independent, with an R^2 of only 0.25. However, the four lowest leaf areas occurred in shade treatments that were fertilized, and they all had high leaf nitrogen (Fig I.1).

The ratio between nitrogen and chlorophyll concentrations averaged 3.7, and this did not vary significantly with shading or with Mg/Fe fertilization treatments. Shade leaves generally have lower nitrogen/chlorophyll ratios than sun leaves (Bjorkman 1981), so the absence of a shade effect was surprising. However, the nitrogen/chlorophyll ratio was lower in trees that received no nitrogen than in trees with moderate or high nitrogen fertilization. Across the broad ranges in canopy

chemistry induced by the treatments, chlorophyll and nitrogen tended to vary together (Fig. I.2).

Photosynthetic Capacity

$A_{rubisco}$ and A_{ci350} (Fig. I.3A) were very highly correlated, with an R^2 of 0.98. The correlation between A_{ci350} and A_{max} was lower (R^2 = 0.80, Fig. I.3B). On the average, stomatal resistance reduced photosynthesis by 47% from what it would have been if stomatal conductance were infinite under our measurement conditions (evaluated from the formula, % limitation = $(A_{ci350} - A_{max})/A_{ci350}$ (Farquhar and Sharkey 1982). Stomatal limitation was slightly higher (49%) for unshaded canopies than for shade-treated canopies (45%); the difference was not significant statistically.

The overall correlation between leaf nitrogen (mg dm^{-2}) and A_{max} was low (R^2 = 0.28). Nitrogen concentration was better correlated with $A_{rubisco}$ (Fig. I.4A), although the overall R^2 was still low (R^2=0.39). Most of the variability came from the four canopies that received the highest level of nitrogen fertilization under shaded conditions; these were the four canopies that had the lowest leaf area (Fig. I.1). When these were removed from the data set the R^2 improved to 0.68. When only the sun-exposed canopies were considered the correlation was still higher (R^2=0.84). The relationship between nitrogen and $A_{rubisco}$ was generally linear, although it appears that at high N, Rubisco activity may level off.

Overall, leaf chlorophyll (mg dm^{-2}) was a better predictor of A_{max} and $A_{rubisco}$ than leaf nitrogen was, with R^2 values at 0.48 and 0.44, respectively (Fig I.4B). This was because of a better relationship between chlorophyll and photosynthesis of the shade-treated canopies. Chlorophyll was not as closely correlated with $A_{rubisco}$ of the

unshaded canopies as nitrogen was, although the relationship was still reasonably good ($R^2 = 0.80$)

Light Absorption

APAR of leaves-plus-stems and APAR of leaves-only varied strongly and nonlinearly as functions of total leaf area. On the average, stems accounted for 17% of total canopy APAR. The variability was higher for the leaves-only data set. For this reason, I used APAR of intact trees in all subsequent analyses, recognizing that a variable amount of the absorbed light would be unavailable for photosynthesis.

I used a non-linear regression approach (SAS 1985) to estimate k in equation 3. The estimated k was 0.48 (standard error = 0.014). A somewhat better fit to the data was obtained by including an intercept in the model: $PAR_{trans} = e^{(k0+kILAI)}$. With this model (Fig. 5), 87% of the variation in PAR_{trans} was explained by LAI. On the other hand, PAR_{trans} and APAR were completely independent of chlorophyll concentration ($R^2 = 0.01$). Adding chlorophyll concentration in a variety of non-linear regression models with LAI (equations 4, 5 and 6) explained no additional variation. In other words, light transmission (and therefore, absorption) was entirely a function of leaf area; the pigment concentration of the leaves varied from chlorotic to very dark green, yet had no measurable effect on the amount of light transmitted.

The data set used to analyze relationships between APAR, leaf area and pigment concentration was twice as large (48 canopies) as the data set for other analyses. This was because each canopy was analyzed both with its full complement of 20 trees and with every other tree removed from the holder. The correlation coefficients from regressions using this data set may be artificially high due to autocorrelation. However, inclusion of the half-canopies in the analyses yielded a much broader range

of leaf areas to test relationships between LAI, chlorophyll, and APAR. The possible autocorrelation would not affect the conclusion that chlorophyll had no measureable effect on APAR.

Whole Canopy Photosynthesis

Whole canopy photosynthesis varied 6-fold across the 24-canopy data set, from about 1 to 6 μmol CO_2 s^{-1} per whole canopy. Total canopy leaf area ranged from just under 0.3 to just over 1.1 m^2; combining the two yielded an average unit leaf photosynthetic rate that varied between 2 and 7.8 μmol m^{-2} s^{-1}. The mean unit leaf photosynthetic rate of shade-treated canopies was 87% of their photosynthetic capacity (A_{max}), while for sun-adapted canopies the unit leaf photosynthetic rate was only 72% of their A_{max}. The difference between these mean values was not statistically significant, although variability was high and may have masked a true difference between shaded and exposed foliage. Some difference makes sense biologically. Unshaded canopies had a higher average leaf area, which would lead to more self-shading. It is also likely that the shade-treated canopies had a lower light compensation point than the unshaded canopies (Bjorkman 1981).

Relationships between whole-canopy photosynthesis and a variety of other variables are illustrated in Fig. I.6A-F. As expected, canopy photosynthesis saturated as leaf area increased, although the overall variability was high (Fig. I.6A). Leaf area explained 56% of the variability in canopy photosynthesis of the shade-treated canopies when fit to a logarithmic model, but for the unshaded canopies photosynthesis was virtually independent of leaf area ($R^2 = 0.07$). The trends are partly due to the narrower range of leaf area among unshaded canopies. The relationship between canopy photosynthesis and APAR was linear (Fig. 6B). Again, the relationship was

much better for shade-treated canopies (R^2 = 0.56) than for unshaded canopies (R^2 = 0.02).

The situation is reversed when canopy photosynthesis is evaluated as a function of photosynthetic capacity (Fig I.6C shows photosynthesis as a function of A_{max}). The closest correlation was with the unshaded canopies . A_{ci350} and $A_{rubisco}$ were almost identical in their relationship to canopy photosynthesis, which is not surprising since they are so closely related to each other. Both variables explained 83% of the variability in photosynthesis of unshaded canopies, but the R^2 was only 0.40 for unshaded canopies. A_{max} was slightly better correlated than A_{ci350} or $A_{rubisco}$ with shade treated canopies (R^2 = 0.47), but slightly lower with the unshaded canopies (R^2 = 0.76). When shaded and unshaded treatments were combined, A_{max} explained 57% of the variability, about 2 percent more than the other two indicators. All three indicators of ϵ tended toward non-linearity. When non-linear models were fit to the data, all correlations improved by 2 to 3 percent.

APAR and photosynthetic capacity were better in combination than either alone at predicting A_{canopy}. The best multiplicative model was A_{canopy} as a function of APAR $\cdot$ $A_{max}^{1/2}$ (Fig. I.6D), with an overall R^2 of 0.73; for shade-treated canopies the R^2 was 0.72 and for unshaded canopies the R^2 was 0.77. A_{ci350} and $A_{rubisco}$ were both better predictors for unshaded canopies; the R^2 for the model A_{canopy} = a + b(APAR $\cdot$ $A_{rubisco}^{1/2}$) was 0.83. Additive multivariate models of the form A_{canopy} = a + b(APAR) + c(ϵ) generally had slightly better explanatory power, with correlations 1 to 3 percent higher than comparable multiplicative models.

Total nitrogen and total chlorophyll content of canopies were related non-linearly to A_{canopy} (Fig. I.6E and F). When fit to logarithmic models, both provided fairly good predictions of A_{canopy} of unshaded canopies, with R^2 values 0.77 and 0.71, respectively. For total nitrogen, correlations were not as good for shade-treated

canopies, with $R^2 = 0.57$, but the relationship between total chlorophyll and A_{canopy} was nearly as good as for shade-treated as for unshaded, with $R^2 = 0.70$.

DISCUSSION

All of the variables in this experiment include a measurement error, and that error reduced the power to test models. A_{canopy} measurements, in particular, included sizeable errors. Determining flow rate through the chambers created one source of error; the flow was turbulent through the exit port, and it was not possible to measure the bulk flow with great accuracy. Also there was variability in the CO_2 concentration at the inlet port, creating considerable noise with respect to the CO_2(in)-C_2(out) signal. The noise due to measurement error is probably at least $\pm$15%. When variability due to respiration is considered as well (higher nitrogen tissues will have much higher maintenance respiration rates), it is not surprising that 20% to 30% of the variability in photosynthesis was not explained by any of the independent parameters I investigated. However, given that at least 20% of the variability is due to other causes, much can be learned from an analysis of the remaining 'explainable' variation.

Although the precision of A_{canopy} measurements was not high, their absolute values are in a reasonable range. When photosynthetic rates are scaled to a unit ground area basis, they range from 4.6 to 35.8 μmol CO_2 m^{-2} ground s^{-1}, with a mean value of 20.4. This compares reasonably well with the diurnal maximum photosynthetic rate of a stand of Sitka spruce with an LAI of 6, measured using eddy correlation techniques at 32 μmol CO_2 m^{-2} ground s^{-1} (Jarvis 1979).

APAR was not a strong determinant of photosynthesis in this study. The null hypothesis (Objective 1) that ϵ is a constant and A_{canopy} is a linear function of APAR

was clearly not true for this experimental system. These results are in part a function of the experimental design. There was a fairly small range of APAR, especially among the unshaded canopies, and I deliberately induced a very broad range of photosynthetic capacity. In natural Douglas-fir communities it is more likely that APAR would be more variable and photosynthetic capacity would be less variable. The advantage of the experimental manipulation is that it highlights the potential impact of varying photosynthetic capacity on whole-canopy function.

The model in equation 1 improved greatly when ϵ was treated as a variable that is dependent on photosynthetic capacity (Objective 2). Rubisco activity ($A_{rubisco}$), photosynthetic potential without stomatal constraints (A_{ci350}), and total photosynthetic capacity including stomatal limitations (A_{max}) all had similar ability to serve as indicators of . However, A_{max} was slightly better overall. This was probably because stomatal limitations to photosynthesis were different in shade-adapted *vs.* sun-adapted canopies, and A_{max} reflects that difference.

If photosynthetic capacity declined through the canopies in direct proportion to the light extinction, one would predict that the slope of a regression relating A_{max} *vs.* to the average unit leaf photosynthetic rate would be unity. In fact, the slope was significantly less than one (0.76), and this is probably why there was a non-linear relationship between A_{canopy} and photosynthetic capacity. I used a trial and error approach to identify appropriate functions relating ϵ to photosynthetic capacity, and a square root function explained the data reasonably well, although there is no theoretical basis for this choice. The results may have been influenced by the use of artificial lights for measurements of photosynthesis, since the artificial light should extinguish more rapidly through the canopy than natural sunlight would. Clearly more information is needed on the variation of photosynthetic capacity through canopy profiles.

To summarize the foregoing discussion: this study demonstrates that A_{canopy} is better modelled using photosynthetic capacity at the top of the canopy as an indicator of ϵ than to treat ϵ as a constant. However it does not demonstrate that photosynthetic capacity at the top of the canopy is equivalent to the biochemical CO_2 fixation capacity of the entire canopy.

Nitrogen and chlorophyll concentrations were both reasonably good predictors of A_{max} (Objective 3), although correlations were not as high as many reported in the literature. In both cases the relationships fell when foliage had been acclimated to shade. This phenomenon has been noted previously (Rose 1989, Chapter 3).

The product of nitrogen or chlorophyll *concentration* and total leaf area is the total nitrogen or chlorophyll *content*. Because leaf area determines APAR, it is not surprising that total nitrogen or chlorophyll content provided fairly good, albeit non-linear, predictions of canopy photosynthesis. Importantly, both were much better than APAR in explaining variability in A_{canopy}.

The absence of a relationship between chlorophyll concentration and APAR (Objective 4) seems counter-intuitive. A probable explanation is that light absorption by each individual needle saturates at a fairly low chlorophyll concentration. Therefore, increases in chlorophyll cause very small changes in APAR compared with increases in total leaf area.

The results of this study have important consequences for interpreting canopy reflectance data from remote sensors. A variety of 'greenness indices' have been developed over the years that combine reflectance signals in red wave bands (influenced primarily by chlorophyll absorption) and near infrared wave bands (influenced primarily by the amount of leafy biomass). Much work has been done to relate various indices to LAI, plant biomass, and APAR. This study suggests that at a given LAI, chlorophyll could vary widely and have little impact on APAR. The change in

chlorophyll, however, would affect the greenness indices and should also indicate changes in the total photosynthetic potential of the canopy. Photosynthetic capacity, on a unit leaf area basis, has virtually never been considered in a remote sensing context, but it could be that greenness indices are actually better indicators of photosynthetic potential than they are of leaf area or APAR. This hypothesis is tested in Chapter 2.

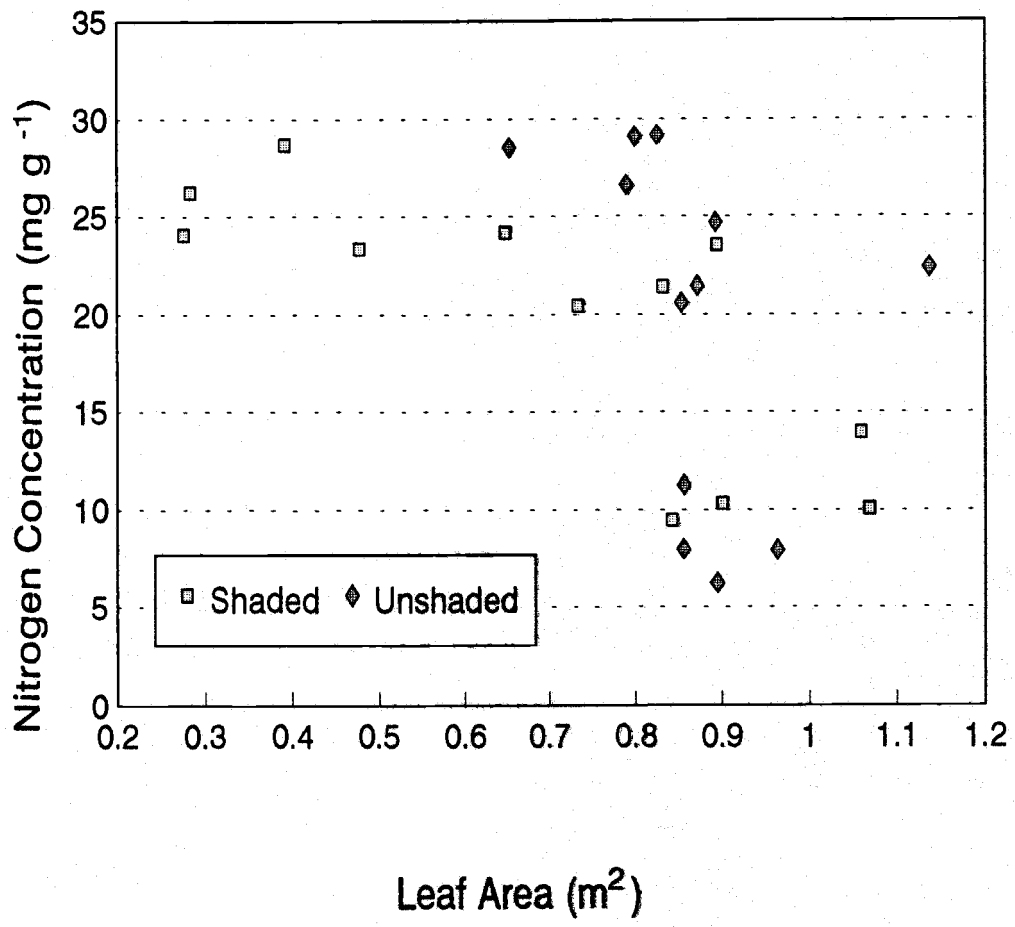

Fig. I.1. Relationships between total leaf area and nitrogen concentration in the experimental canopies.

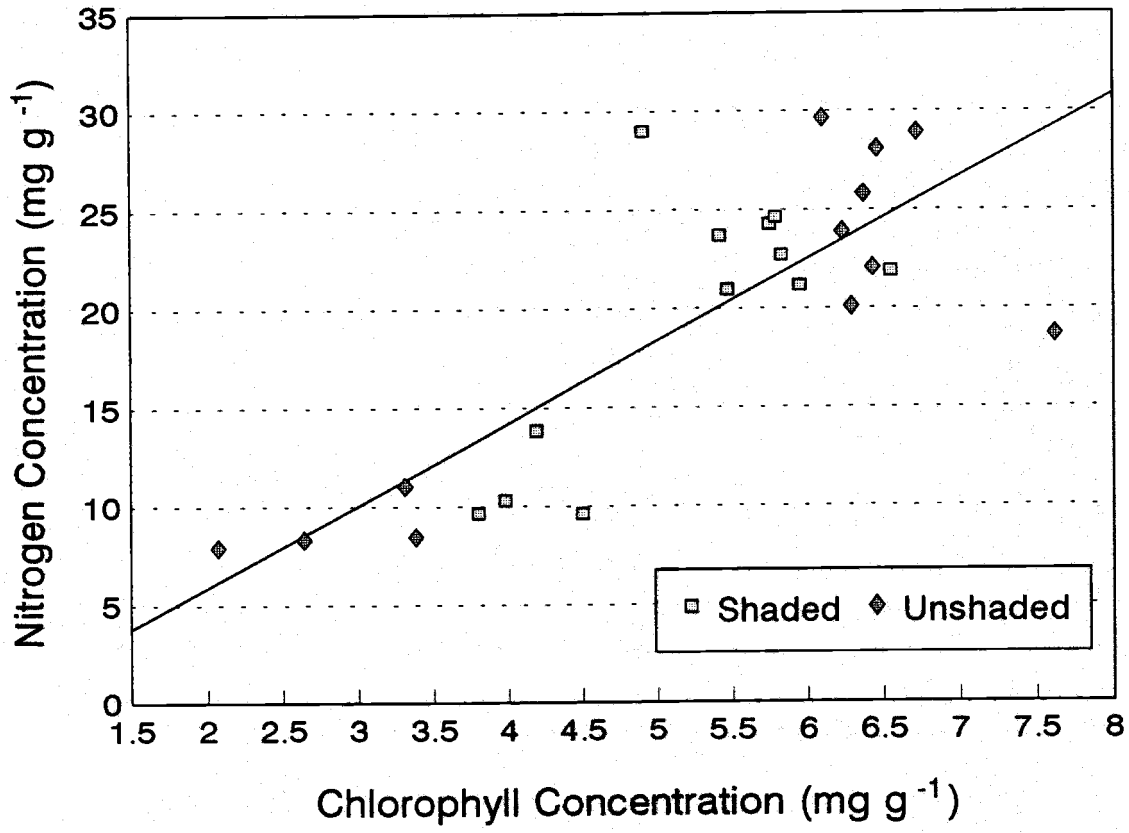

Fig. I.2. Relationships between chlorophyll and nitrogen concentrations of shaded and unshaded foliage. R^2 overall = 0.80, R^2 shaded = 0.56, R^2 unshaded = 0.73. Regression lines are not significantly different for shaded and unshaded treatments.

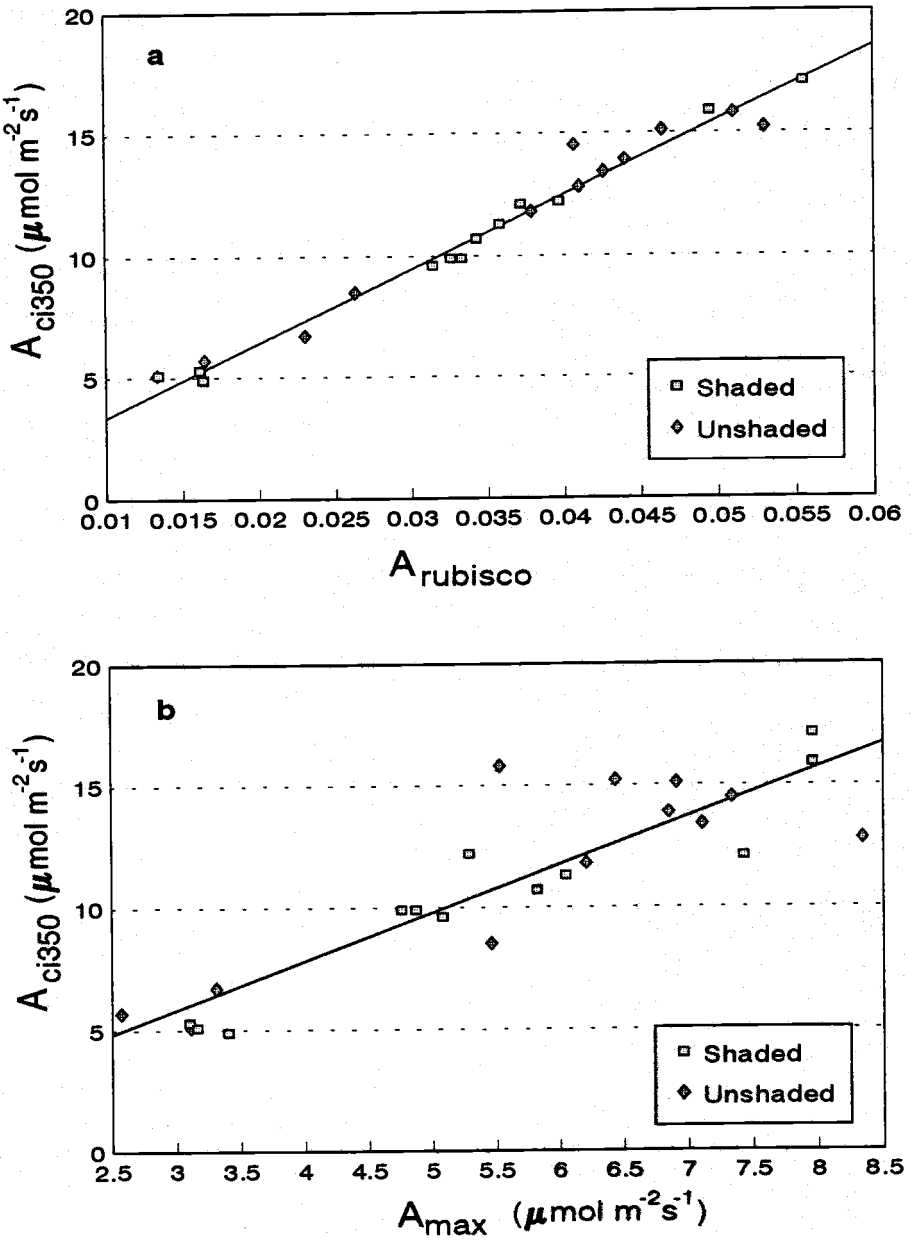

Fig. I.3. Relationships among three measures of photosynthetic capability. See text for definitions of terms. a. R^2 overall = 0.98, R^2 shaded = 0.99, R^2 unshaded = 0.97 b. R^2 overall = 0.80, R^2 shaded = 0.95, R^2 unshaded = 0.70. Regression lines are not significantly different for shaded and unshaded treatments.

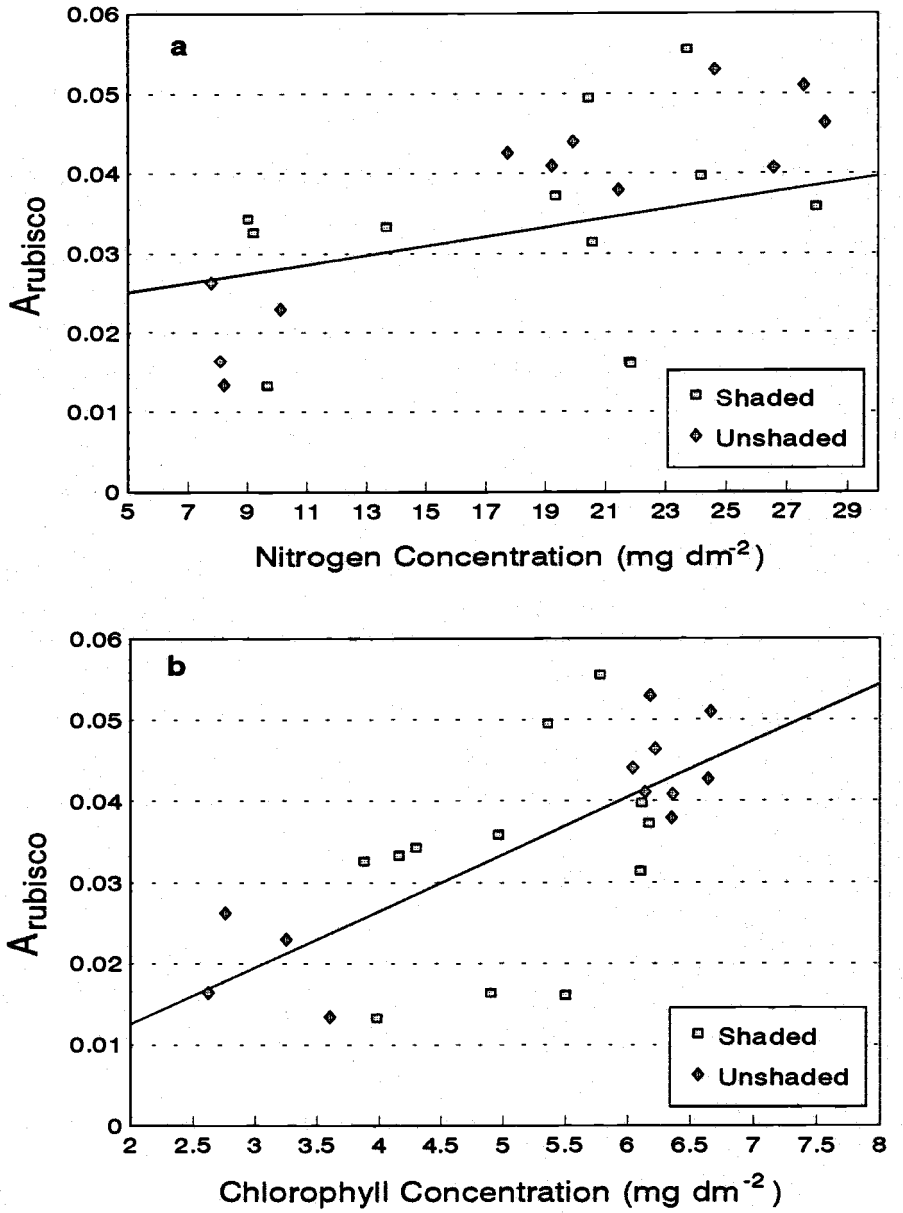

Fig. I.4. Relationships between leaf nitrogen (a) and chlorophyll (b) and the initial slope of A/C_i curves (Rubisco activity). a. R^2 overall = 0.39, R^2 shaded = 0.09, R^2 unshaded = 0.82. b. R^2 overall = 0.48, R^2 shaded = 0.15, R^2 unshaded = 0.15. Regression lines were not significantly different for shaded and unshaded trees.

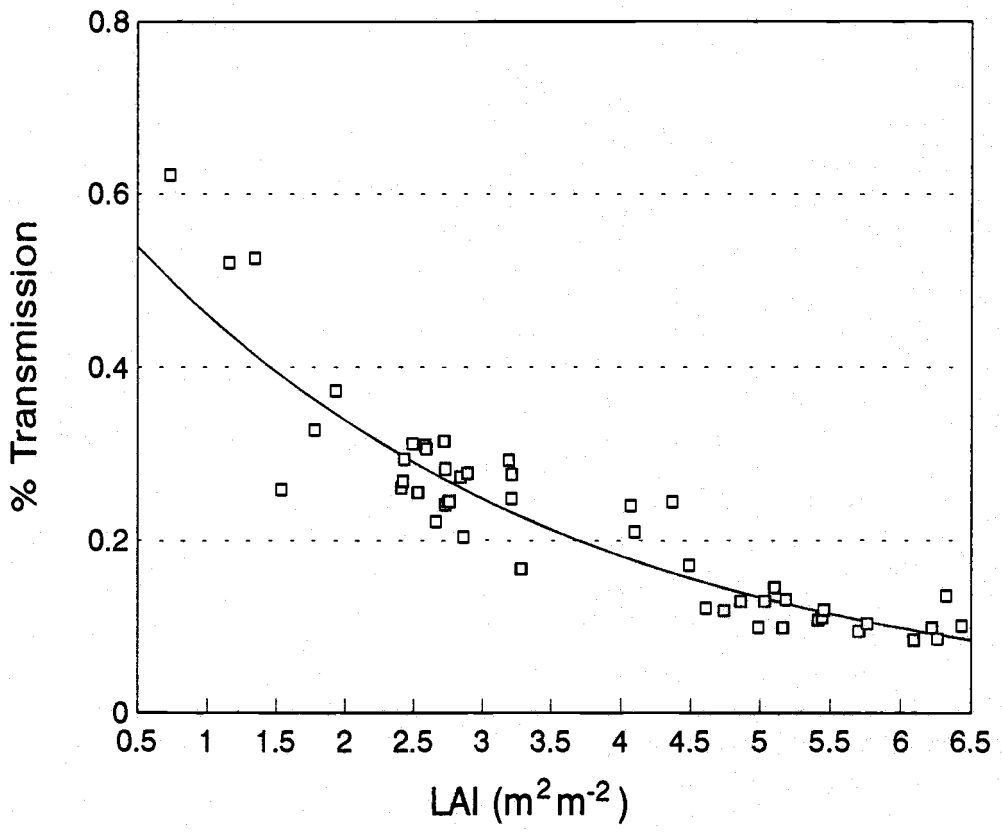

Fig. I.5. Percent transmission of light through canopies as a function of LAI. $R^2 = 0.87$ for the model $PAR_{trans} = e^{(k0+k1LAI)}$.

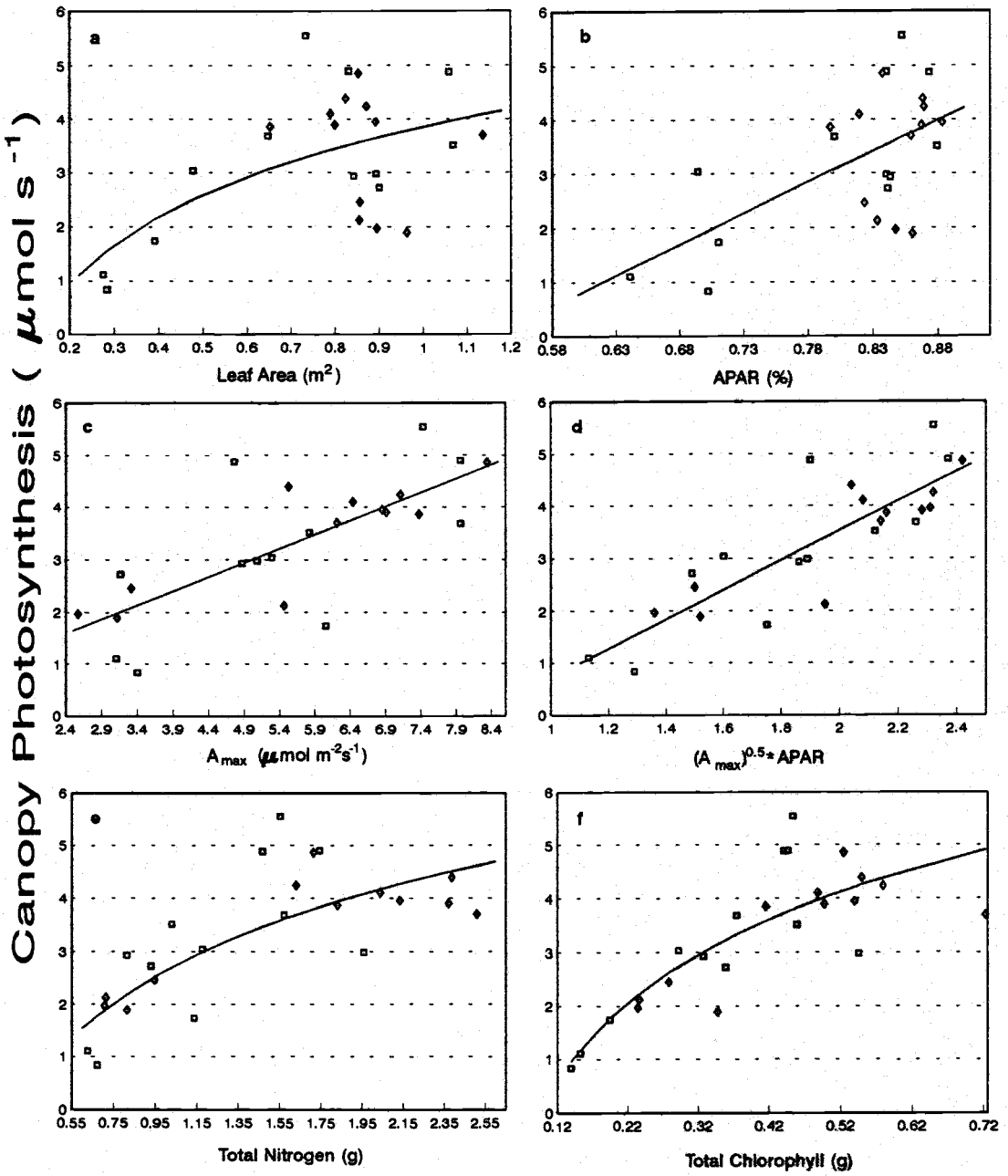

Fig. I.6. Relationships between canopy photosynthesis and (a) total leaf area, (b) APAR, (c) photosynthetic capacity, (d) a model combining APAR and photosynthetic capacity, (e) total nitrogen content, and (f) total chlorophyll content. a. R^2 over all = 0.31, R^2 shaded = 0.56, R^2 unshaded = 0.02. b. R^2 overall = 0.36, R^2 shaded = 0.56, R^2 unshaded = 0.02. c. R^2 overall = 0.57, R^2 shaded = 0.47, R^2 unshaded = 0.76 d. R^2 overall = 0.73, R^2 shaded = 0.72, R^2 unshaded = 0.77. e. R^2 overall = 0.59, R^2 shaded = 0.57, R^2 unshaded = 0.78. f. R^2 overall = 0.68, R^2 shaded = 0.70, R^2 unshaded = 0.71.

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Chapter II

RELATIONSHIPS BETWEEN REMOTELY SENSED VEGETATION INDICES AND CANOPY PHOTOSYNTHETIC POTENTIAL

ABSTRACT

In order to clarify the interpretation of remotely sensed signals from vegetation canopies, I designed a laboratory experiment in which measurement conditions could be controlled carefully. The experimental design minimized variability in reflectance signals due to background, shadow, and illumination. Small canopies of Douglas-fir seedlings were given shade and fertilization treatments for 14 weeks to induce a range of canopy chemistry and photosynthetic potential. Leaf area was manipulated independently from chemistry so their separate effects on reflectance spectra could be analyzed. The specific objective of the experiment were: (1) Determine whether reflectance of visible light (400-700 nm) and position of the red edge are more closely related to chlorophyll concentration or to chlorophyll content (content is the product of concentration and total leaf area). (2) Evaluate methods for predicting chlorophyll content and concentration from reflectance spectra and derivatives of reflectance spectra. (3) Test the hypothesis that remotely sensed vegetation indices derived from reflectance of red and near infrared light (the simple ratio, SR, and the normalized difference vegetation index, NDVI) are better indicators of canopy photosynthetic potential than they are of leaf area index (LAI, m^2 leaf area/m^2 ground area) or of the potential to absorb photosynthetically active radiation (APAR). (4) Evaluate the effect of using different bands in the visible range in calculations of SR and NDVI.

I found that reflectance throughout the visible region was sensitive to chlorophyll concentration. If total content of chlorophyll changed (due to changes in leaf area) while concentration remained the same, there was little change in reflectance between 400 and 700 nm. On the other hand, the position of the red edge was more closely related to total chlorophyll content. Chlorophyll concentration was poorly

correlated with reflectance at the absorbance maxima in blue and red wavebands. The best predictors I found for chlorophyll concentration were the first derivative at 645 nm and the distance (in nm) between the blue and red reflectance minima (R^2 = 0.83 and 0.85, respectively).

Changes in both LAI and chlorophyll concentration caused variation in SR and NDVI. Therefore, the two indices were poor predictors of leaf area in this study due to broad variation in chlorophyll over narrow ranges of LAI (R^2 between SR and LAI=0.37; R^2 between NDVI and LAI=0.36). In an earlier study (Chapter 1) I found that APAR was almost entirely a function of leaf area; variability in chlorophyll concentration had no measureable impact on light absorption. SR and NDVI, therefore, were not closely correlated with APAR (R^2 between SR and APAR = 0.58; R^2 between NDVI and APAR = 0.60). Because canopy photosynthetic potential and the vegetation indices both varied in response to changing leaf area and chlorophyll concentration, the vegetation indices were better correlated with canopy photosynthetic potential than they were with LAI or APAR (R^2 between SR and photosynthetic potential = 0.68, R^2 between NDVI and photosynthetic potential = 0.67).

When different visible bands were used to calculate SR or NDVI, their correlations with canopy features changed. When NDVI was calculated with a narrow red band between 670 and 675 nm, it was less sensitive to variations in chlorophyll, and correlations with LAI and APAR improved. When NDVI was calculated using a broad green band (500 - 600 nm), it was more sensitive to chlorophyll concentration, and correlations with photosynthetic capacity improved.

INTRODUCTION

Remote sensing is emerging as a powerful tool for plant biologists interested in regional and global scale phenomena (Matson and Ustin 1991, Roughgarden *et al.* 1991, Ustin *et al.* 1991, Wickland *et al.* 1991). Analytical procedures that were originally developed by geographers to map extent and type of vegetation cover are being applied to studies of vegetation structure and function. Paramount among these are vegetation indices derived from the amount of visible (VIS) and near-infrared (NIR) light reflected from vegetation canopies.

Many studies have shown empirical relationships between remotely sensed vegetation indices and structural characteristics of vegetation, such as biomass and leaf area index (LAI, m^2 leaf area/m^2 ground area). Some analyses have related vegetation indices to more functional attributes, such as photosynthetic potential. Unfortunately, correlations do not necessarily imply causal relationships. Most studies have been conducted in the field, where variables such as LAI, chlorophyll concentration and water content are often auto-correlated. Because of these multiple sources of variation, it can be difficult to analyze the effects of single factors. Another difficulty in field studies is accurate measurement of the properties of vegetation under study, such as concentration and content of foliar chemicals (Curran 1989).

In order to clarify the interpretation of remotely sensed signals from vegetation, I designed a laboratory experiment where measurement conditions could be controlled and accurate measurements could be made of leaf chemistry and leaf area. I used small canopies which had independently varying leaf area and pigmentation to assess whether reflectance measurements could (1) predict chlorophyll concentration and/or content, (2) predict LAI and light absorbance properties, and (3) relate to the photosynthetic potential of the canopy.

I designed the experiment so that the effects of shadow, illumination angle, specular reflectance and background on the reflectance signal were minimal. These parameters are important sources of variability, and their effects must be understood in order to interpret remotely sensed vegetation indices. However, in order to understand the reflectance properties of the vegetation alone, I tried to eliminate these peripheral effects.

BACKGROUND

Reflectance Properties of Leaves and Canopies.

Green vegetation has a unique reflectance signature through the VIS and NIR regions of the electromagnetic spectrum (Fig. II.1a). Plants absorb very little NIR light, and NIR reflectance is high due to multiple interfaces of intercellular air and water-filled cell walls in leaves. The refractive indices of air and water are different, causing light to scatter (Knipling 1970). Typically, 40 to 60 percent of incident NIR light is scattered upward, or reflected (Knipling 1970). Cell hydration, the amount of cell surface relative to intercellular space (related to cell size and shape), and leaf area all affect NIR reflectance. Intracellular components such as nuclei and cytoplasmic substances also contribute to NIR scattering, although this is only about 8% of total (Gausman 1977). Within a single species with well hydrated cells, NIR reflectance should vary primarily as a function of leaf area.

Reflectance of visible light tends to be very low due to absorption by plant pigments. Chlorophylls a and b and carotenoids absorb blue light; red (R) absorption is only by chlorophylls (Gates *et al.* 1965). Because plant pigments do not absorb green light strongly, there is relatively more reflectance of green light.

In a plant canopy, pigment concentration is not the same as pigment content. Concentration is the amount of pigment per unit leaf area or mass. Content is the product of average concentration and total area or leaf mass. A canopy with high leaf area and chlorotic leaves might have the same pigment content as a canopy with low leaf area and high pigment concentration. Which is more influential in VIS absorbance? In studies with stacked leaves, Horler *et al.* (1983) found that when chlorophyll concentration and leaf area were manipulated independently, VIS and NIR reflectance were uncorrelated. These results suggest that VIS reflectance responds to concentration, not content, but there is little experimental evidence on the canopy scale.

The Simple Ratio and Normalized Difference Vegetation Index

Among the most common vegetation indices are the simple ratio (SR; NIR/R) and the normalized difference vegetation index (NDVI; (NIR-R)/(NIR+R)), although many other combinations of wavebands have been investigated (Tucker 1979). An important rationale for combining R and NIR bands is that vegetation and soils have dramatically different reflectance patterns in these bands, so these combinations allow good separation of plant from non-plant cover. These indices are usually computed from broad reflectance bands; the precise wavelength ranges for R and NIR depend on the type of sensor used. Some analyses use average VIS reflectance instead of R reflectance (e.g. Goward and Dye 1987, Sellers 1985, 1987, Huemmrich and Goward 1990). It has not been established whether the range and position of the bands (e.g. a red band that ranges from 600 - 675 nm, 625 - 700 nm or 670 - 690 nm) makes a significant difference to SR and NDVI.

Over twenty years ago, Jordan (1969) observed that because plants absorb visible but not NIR light, the ratio between visible and NIR light that penetrates a canopy should be related to the leaf area index. Since then, both NDVI and SR, derived from visible and NIR light reflectance rather than transmission, have been related to a number of physical characteristics of vegetation, including biomass (Tucker 1979), chlorophyll content (Tucker 1979), and LAI (e.g. Curran 1983, Asrar et al. 1984, Running et al. 1986). Theoretical and experimental work indicates that NDVI is often proportional to the fraction of incident photosynthetically active radiation (PAR, 400-700 nm) that is absorbed by a canopy (APAR) (Kumar and Monteith 1981, Hatfield *et al.* 1984, Asrar et al. 1984, Goward et al. 1985, Sellers 1985, 1987).

More recently, relationships have been shown between these vegetation indices and vegetation processes. When NDVI obtained from NOAA weather satellites is summed over a full year, it correlates well with the annual productivity of natural vegetation (Tucker *et al.* 1981, Goward *et al.* 1987, Running and Nemani 1988). Tucker *et al.* (1986) and Fung *et al.* (1987) reported correlations between regionally-averaged NDVI and regional variation in CO_2 concentrations, suggesting that seasonal changes in NDVI can be related to regional photosynthetic rates. Weekly integrations of NDVI compared well with simulated estimates of weekly photosynthesis (Running and Nemani 1988), although correlations decreased in drought-stressed areas.

The correlation between NDVI and productivity has been associated with the relationship of both of these factors with APAR (Kumar and Monteith 1981, Hatfield *et al.* 1984, Asrar *et al.* 1984, Goward 1989). There is good evidence (e.g. Monteith 1977) that growth of many crops can be described by the equation:

$$(1) \qquad NPP = \epsilon \cdot APAR$$

where NPP is above-ground net primary productivity and ϵ is visible light-energy-to-biomass conversion efficiency. If ϵ is constant and if NDVI is proportional to APAR, then it follows that integrated NDVI should be a good predictor of productivity.

The 'Red Edge' Analysis

The 'red edge' is the position on the electromagnetic spectrum of the inflection point that occurs in the rapid transition between red absorption and near-infrared reflectance. The position of the inflection point can be determined from a first or second derivative of the reflectance spectrum (Fig 1b).

The position of the red edge has been related to chlorophyll (Horler *et al.* 1980, 1983); there is a shift to shorter wavelengths (toward the blue) with decreasing chlorophyll. In some studies (e.g. Horler *et al.* 1983) the position of the red edge correlated well with chlorophyll concentration of leaves, and in others (e.g. Curran *et al.* 1990) the red edge correlated with total chlorophyll content of stacked branches. Environmental stresses of various kinds often reduce both the concentration of chlorophyll and total leaf area; for this reason the exact relationship with the red edge shift and chlorophyll has remained unclarified in field studies. Because of the relationship between environmental stress and the concentration or content of chlorophyll, shifts in the position of red edge have been used to interpret plant stress and forest decline (e.g. Collins 1978, Rock *et al.* 1986, Ustin *et al.* 1988).

Canopy Photosynthetic Potential and Leaf Photosynthetic Capacity

Canopy photosynthetic potential is the photosynthetic rate of a canopy (which may be normalized per unit ground area) under 'optimum' environmental conditions. Leaf photosynthetic capacity is the photosynthetic rate *per unit leaf area* under saturating light, ambient CO_2 and 'optimum' conditions for other environmental factors.

The difference between leaf photosynthetic capacity and canopy photosynthetic potential is analogous in some ways to the difference between chlorophyll concentration and chlorophyll content. However, unlike the chlorophyll concentration/content relationship, canopy photosynthetic potential is not the simple product of leaf photosynthetic capacity and total leaf area. This is because canopies are rarely light saturated, so many of the leaves in a canopy may not photosynthesize at their potential rates even when light at the top of a canopy is high. The precise relationship between leaf and canopy photosynthesis capacity is complex: leaf photosynthetic capacity declines with canopy depth, actual leaf photosynthesis declines hyperbolically with decreasing light level, and light is extinguished exponentially through a canopy profile. In addition, atmospheric humidity and temperature can vary greatly within a canopy, especially if the canopy is short and aerodynamically smooth.

There are a number of mathematical models of varying complexity that describe leaf and canopy level photosynthesis. Implicit in the logic relating APAR to above-ground productivity (discussed above) is the assumption that canopy photosynthesis varies only as a function of the amount of PAR absorbed. If this is true, photosynthetic capacity of individual leaves within a canopy or in different canopies must vary in direct proportion to the average PAR absorbed by those leaves.

Sellers (1985, 1987) and Tucker and Sellers (1986) combined radiative transfer models with leaf-levels model of photosynthesis to derive theoretical relationships between vegetation indices and canopy photosynthetic potential. Their photosynthetic models were of the general form:

$$(2) \qquad A = (a_1 \cdot I)/(b_1 + I)$$

where A is net CO_2 assimilation, a_1 is a coefficient describing photosynthetic capacity under light saturating conditions, b_1 is a coefficient describing quantum efficiency in low light, and I is the incident flux of PAR. Sellers (1985, 1987) and Tucker and Sellers (1987) point out that when I is small, A becomes nearly proportional to I, with a slope a_1/b_1. By assuming that a_1 and b_1 are constants, and also that the average radiative flux within a canopy is small, they demonstrated that the photosynthetic potential of a canopy should be a linear function of absorbed light.

In Chapter 1 I demonstrated that leaf-level photosynthetic capacity (analagous to a_1 in equation 2) of Douglas-fir foliage could vary widely when trees had been fertilized differently. The variable photosynthetic capacity had a large impact on whole canopy photosynthesis. Whole canopy photosynthesis was better modeled by the product of the photosynthetic capacity assessed at the top of the canopy and APAR than by either alone. Furthermore, I determined that chlorophyll concentration was positively correlated with photosynthetic capacity when foliage was grown in sunlit conditions. Interestingly, visible light absorbed by the canopy (APAR) was strictly a function of the interspersed leaf area. Variation in chlorophyll concentration had no statistically significant effect on measured APAR.

HYPOTHESIS AND OBJECTIVES

All three of the indices discussed above combine R and NIR reflectance. In the cases of NDVI and SR the mathematical combination is explicit. In the case of the red edge, the position of the inflection point is an interaction between R absorption and NIR reflectance. Because reflectance of red light is largely a function of chlorophyll concentration (decreased reflectance associated with increased chlorophyll) and reflectance of NIR is closely related to leaf area (increased reflectance associated with increased leaf area), I reasoned that together, when expressed as a ratio, they should be good predictors of the photosynthetic potential of a canopy.

A similar hypothesis, relating to growth rather than photosynthesis, was first advanced by Steven *et al.* (1983). They reasoned that "if the efficiency of photosynthesizing leaves is directly related to their chlorophyll content and if chlorophyll loss is the main source of variation in ϵ during a season, then the present IR/R spectral ratios may in fact be more closely related to APAR*ϵ than to APAR alone" (p. 332, substituting my notation).

The primary objective of this study was to test this hypothesis. I also analyzed relationships between reflectance spectra and biophysical characteristics of plant canopies to clarify interactions. Specific objectives were:

1. Determine whether reflectance of visible light and the position of the red edge are more closely related to chlorophyll concentration or to chlorophyll content.
2. Evaluate methods for predicting chlorophyll content and concentration from reflectance spectra and derivatives of reflectance spectra.
3. Test the hypothesis that remotely sensed measures of SR, NDVI and the red edge are better indicators of canopy photosynthetic potential than they are of LAI or APAR.

4. Evaluate the effect of using different bands in the visible range in calculations of SR and NDVI.

METHODS

Plant Material

Small canopies of Douglas-fir seedlings served as the observational units for this study. A whole canopy consisted of 20 seedlings. Each seedling was planted in a separate tube (5 cm diameter and approximately 25 cm long), and the 20 trees that constituted a canopy were attached together in a 4-tree x 5-tree matrix with a holder at the top of the tubes. This configuration permitted individual trees to be removed and replaced from the canopy block. Throughout this Chapter, a complete block of trees, including the planting tubes, will be referred to as a 'canopy'. The canopies averaged about 1 m in total height, including planting tubes, and the length and breadth of the foliage average about 0.4 m on a side.

Twenty-four canopies were given shade and fertilization treatments for 3 1/2 months to induce a broad range of photosynthetic potential. Details are described in Chapter 1. Measurements of canopy photosynthesis, APAR, leaf area and chlorophyll are also described in detail in Chapter 1. All of these measurements were made on canopies with every other tree removed (10 seedlings; 'half canopies') as well as on whole canopies with 20 seedlings. APAR was calculated from measurements of percent transmittance and percent reflectance of PAR, using the formula APAR = 100% - $PAR_{transmitted}$ (%) - $PAR_{reflected}$ (%) (see Chapter 1 for details). The term 'APAR' in this study refers the fraction of incident light the canopy can absorb (sometimes termed *f*APAR in other studies), not a total amount of light.

Reflectance Measurements

Canopy reflectance was measured with an SE-590 spectroradiometer fitted with a 15° FOV lens. This instrument has approximately 10 nm band widths with 3 nm peak-to-peak distance between 375 and 1100 nm. I used a hemispherical illumination system (Williams and Wood 1987) to provide diffuse light at stable levels at the target surface. This illumination system minimized shadows and specular reflectance on the canopy surface. Black cloth surrounding the system prevented entry of stray light. The system was configured so that the base of the hemispherical light source was 1 m from the top of the canopy. The SE-590 was mounted about 10° off nadir, 0.63 m from the center of the canopy. With this configuration the long axis of the field of view at the canopy surface was about 0.18 m. I ensured through experimental tests that the field of view was always was well within the dimensions 0.4 m x 0.4 m dimensions of the canopy surface.

Canopies were placed one at a time on a revolving platform beneath the illumination system. Because canopy height varied slightly, thin black boards were added under the planting tubes of each canopy so that the canopy top was the same distance from the radiometer and light source for each measurement. Each spectral observation consisted of a total of 64 scans; 16 scans were accumulated from each of four positions, with a 90° rotation between each set. Two reference scans were obtained before and after each set of target scans. For the reference scans, a barium sulfate reference panel was positioned in the same location as the surface of the canopies.

The 64 scans from each canopy were averaged, as were the four reference scans. Radiance from the reference panel was assumed to represent 100% reflect-

ance; percent reflectance from the canopy was calculated for each wave band by dividing radiance from the canopy by radiance from the reference panel. I used soft ware developed by Moon Kim of the Goddard Space Flight Center for these calculations. As with APAR measurements, canopy reflectance was measured with every other tree removed ('half canopies') as well as on whole canopies.

The 'background' from this measurement configuration is essentially an infinite absorber. In a preliminary experiment, reflectance was measured from an empty planting block (20 black tubes filled with soil but without trees), placed 1.75 m from the hemisphere (in the same position that an experimental canopy would occupy). Reflectance never exceeded 3% in any waveband across the measurement spectrum.

Data Processing and Statistics

I computed first difference spectra (approximating derivative spectra) after importing the reflectance files into a spreadsheet, as described by Yoder and Daley (1990). Except where noted otherwise, NDVI and SR were calculated using the average reflectance between 625 and 675 nm for R and between 800 and 900 nm for NIR. In order to evaluate the impact of replacing the red band with other visible wave bands, NDVI was also calculated using average reflectance of other bands. The following alternative bands were used: Broad visible (400-700 nm), green (500-600), narrow green (565-575 nm), red (600-700 nm), and narrow red (671-674). The narrow green and red bands were chosen to represent regions of high and low correlation with chlorophyll concentration (see RESULTS).

The observational unit of this experiment is the canopy. The total sample size was 48, which resulted from using 24 full canopies with 20 trees each, and the same 24 with every other tree removed. This procedure creates observational interdepend-

ence (from the whole-canopy/half-canopy pairs) in the data set (Ripple *et al.* 1986). The interdependence does not affect estimation of regression slopes and intercepts, but it may cause inflation of the coefficient of determination (R^2) (Pindyck and Rubinfeld 1981). Still, relative comparisons can be made among regressions for the same data set to evaluate which model explains the greatest amount of variance (*cf.* Ripple 1986). The R^2 values reported here are for the purpose of making these relative comparisons.

RESULTS

Chlorophyll

The effects of changing chlorophyll concentration on canopy reflectance are illustrated in Fig. II.2. Increased chlorophyll caused decreased reflectance throughout the visible range, but had practically no impact on NIR reflectance. Higher concentration of chlorophyll caused little change in reflectance at the red and blue absorbance masima, although the absorbance troughs became more broad. Fig. II.3a, which is the result of correlation analysis for all canopies, also illustrates that reflectance at the absorbance maxima was not strongly affected by varying chlorophyll concentration.

Chlorophyll concentration was predictable from several features of the reflectance spectra (Table II.1). When reflectance was averaged over broad bands, green reflectance was a much better predictor than red or blue, red was nearly equivalent to the average of the entire visible range, and blue reflectance was a very poor predictor. Fine-resolution analysis improved predictive power (Table II.1, Fig. II.3b). The width of the green peak, evaluated as the difference in nm between the wavelengths in the blue and red where the first derivative equaled zero, was an especially good pre-

dictor of chlorophyll concentration.

Chlorophyll concentration was *not* well correlated with the position of the red edge. However, the red edge was the best predictor I found of total chlorophyll content (R^2=0.73). This compares with an R^2 of 0.62 and 0.51 for SR and NDVI, respectively.

Leaf Area and APAR

Fig. II.4 illustrates how a reflectance spectrum was affected by removal of half of the trees from a typical canopy. This procedure did not change chlorophyll concentration, but total chlorophyll content was reduced by about half. The visible regions of the spectra are very similar, and as expected, there was a significant change in the NIR. Correlelograms for both leaf area and APAR (Fig. II.5) support the conclusion that the NIR is the best region for predicting change in LAI. Leaf area was linearly related to NIR reflectance (R^2=0.68) and APAR was non-linearly related (R^2=0.81) (Fig. II.6).

Reflectance from any part of the visible range was insignificant when included with NIR reflectance in a multiple regression to predict APAR or LAI. In fact, SR and NDVI, which are calculated from both NIR and R, did not predict LAI or APAR as well as the NIR reflectance alone (Figs. II.7., II.8). This is because the variable chlorophyll concentration affected R, and therefore SR and NDVI, whereas variable leaf area at constant chlorophyll concentration resulted in essentially no change in R.

Canopy Photosynthesis

The correlation between NDVI and canopy photosynthesis (Fig. II.9) was better than the correlation between NDVI and APAR (Fig. II.8). NDVI, SR and the

red edge had similar predictive power to explain canopy photosynthesis. In all of the relationships in Fig. II.9, a linear model was a reasonable approximation to the data trends, and there was no clear justification for a non-linear model.

Calculating NDVI with Alternative VIS Bands

When NDVI was calculated using alternative VIS bands instead of the 525-575 nm red band, different values were obtained. Typically the range of these alternative NDVI values was slightly less than 10% of the mean value. For example, the NDVI calculated using a narrow green band (565-575 nm) was 0.79 for one of the canopies, but NDVI calculated using a narrow red band (671-674) for the same canopy was 0.86. The correlations between NDVI and APAR and between NDVI and photosynthsis were strongly dependent on the visible band used to calculate NDVI (Fig. II.2).

DISCUSSION

Chlorophyll Concentration

Chlorophyll and leaf area had almost independent effects on reflectance spectra; the reflectance spectra through the VIS range were related to chlorophyll concentration. Changes in leaf area, which would change total chlorophyll content, had little impact on VIS reflectance.

Correlations between chlorophyll concentration and percent reflectance were low at the absorbance maxima. Similar results have been shown previously (Yoder and Daley 1990, J. Dungan, personal communication). The reason for this phenome-

non probably stems from the negative exponential relationship between absorbance and concentration of the absorber. *In vivo*, there are a wide variety of chlorophyll-protein complexes (CPX's), with varying absorbance properties. The greatest concentration of CPX's absorb at the absorbance maximum; the concentration of absorbers declines at wavelengths away from the maximum. Therefore, as total chlorophyll concentration increases, the marginal change in absorbance is least at the absorbance maxima. The absorbance maxima are the best place to detect changes in chlorophyll ranging from none to very little. They are the worst place to detect changes ranging from moderate to high concentrations.

The 580-680 nm band of the AVHRR sensor is often described as a good band for detecting chlorophyll. For most green vegetation, a narrower band of slightly shorter wavelengths (e.g. 550 - 600 nm) would probably produce better correlations between reflectance and chlorophyll concentration. This analysis, of course, is based on the characteristics of the vegetation only. Confounding effects of background could alter the conclusion.

Correlations with first derivatives were highest at 500, 645 and 687. The reason for the good correlations at these wavelengths is probably because they define average edges of peaks. With increasing chlorophyll, the blue and red absorption troughs become broader, the edges of the green peak move closer together, and the red edge shifts toward the NIR. As this happens, the slopes at the average edges become flatter. This phenomenon also accounts for the good correlation between the breadth of the green peak and chlorophyll concentration.

The derivatives were about 20% better than percent reflectance at even the best wavelengths in explaining variation in chlorophyll. An advantage of derivative spectroscopy in remote sensing is that it can help separate reflectance signals due to targets from other sources of variation (Hall and Huemmrich 1991, Wessman 1991).

However, in this experiment such confounding was minimal. Derivatives improved predictive power because variations in chlorophyll affected the forms of reflectance curves more than the percent reflectance at any particular wavelength.

Total Chlorophyll Content

The position of the red edge correlated well with total chlorophyll content, but not with chlorophyll concentration. Curran *et al.* (1990) also found that the red edge of spectra from stacked branches correlated with total chlorophyll content. Horler *et al.* (1983) showed with leaf stacking experiments that increased layers of leaves at the same chlorophyll concentration shifted the inflection point to the right. They explained that the position of the red edge should be a function both of leaf area and chlorophyll concentration because light penetration through the leaf layers increases with increasing wavelength between 700 and 800 nm due to greater scattering. As more layers of leaves are added, the effective pigment concentration is higher at longer wavelengths because of the longer path length. The same phenomenon probably occurs at the canopy scale, and explains the results of this study.

Vegetation Indices and Canopy Photosynthetic Potential

Iverson *et al.* (1989) wrote, "Mounting evidence suggests that remotely sensed spectral data may become as successful, if not more successful, at estimating forest function (e.g. photosynthesis or evapotranspiration) than forest structure (e.g. biomass or leaf area)." The results of this study concord with their assessment.

This study illustrates the importance of chlorophyll concentration as an influential component in remotely-sensed vegetation indices. In a companion study (Chapter

1), chlorophyll concentration was positively correlated with the photosynthetic capacity of foliage. If all else remains constant (e.g. leaf area, leaf arrangement, leaf water content, soil characteristics), increased chlorophyll concentration should be associated with increased photosynthetic potential of the canopy, decreased VIS reflectance, unchanged NIR reflectance, little or no change to APAR, and increased SR, NDVI and red edge position. Under these conditions the remotely-sensed indices are better predictors of canopy physiological potential than they are of LAI or APAR.

Tucker and Sellers (1986) previously related 'chlorophyll density' (analogous to my definition of 'chlorophyll content') to the 'photosynthetic capacity of the plant canopy'. However, in their model chlorophyll density is proportional to LAI because chlorophyll concentration is considered constant. Also, their modeled biophysical functions, such as photosynthesis, depend only on the amount of PAR absorbed. Leaf-level photosynthetic capacity was considered constant. In simplified form, the logic of their model is that chlorophyll density is proportional to LAI, which determines APAR, which in turn determines photosynthesis; therefore chlorophyll density is related to canopy photosynthetic potential.

My experimental evidence led to the same conclusion through an alternative route. Canopy photosynthetic potential was better described as the product of photosynthetic capacity and APAR than either alone. The vegetation indices also varied with both chlorophyll concentration and APAR, and were therefore good predictors of canopy photosynthetic potential. As predicted by Steven *et al.* (1983), the spectral ratios combining R and NIR were more closely related to APAR $\cdot \epsilon$ than to APAR alone.

The Impact of Using Different VIS Bands in Calculating NDVI

This study shows that indices like SR and NDVI are sensitive to the wavebands that are used in computation. When NDVI was calculated using a broad red band (600-700 nm), it was very similar to an NDVI calculated using the entire VIS region (400-700 nm). If a broad green or narrow red band were used, however, the results were different. Because the green band was more influenced by chlorophyll, it resulted in an improved correlation between NDVI and photosynthetic potential, but a decreased correlation between NDVI and APAR. At the opposite extreme, reflectance in the 670-675 band was influenced far less by changing chlorophyll concentration. An NDVI calculated using this narrow red band was a better predictor of APAR, but correlations with photosynthetic potential were reduced.

Caveats and Needs for Future Work

Controlled studies like this one isolate effects of single factors in order to understand them better. They complement but do not replace field studies that involve multiple factors. For example, the importance of chlorophyll in this study is in part a function of the experimental design. Fertilization treatments in the study created a very broad range of photosynthetic capability and chlorophyll concentration over a relatively narrow range of LAI; this combination is unlikely in the natural world. Experiments are needed that establish how photosynthetic capacity varies in natural environments, especially in relation to leaf area and illumination history.

The good correlation between NIR reflectance and leaf area shown here does not imply that NIR alone would be a good predictor of LAI in the field. If a variable background contributed to the overall reflectance, the correlation between LAI and

NIR would decrease, and the value of ratioing NIR and VIS would become more apparent because it tends to normalize the data and cancel out some sources of variation. Field and modeling studies are needed that consider how the effects of variable chlorophyll concentration in addition to variable background and leaf area affect canopy reflectance.

This study demonstrates that remotely sensed vegetation indices are more closely related to physiological potential than to physical characteristics. It does not provide a 'best' index for remotely sensing photosynthetic potential. For the Douglas-fir in this study, chlorophyll concentration correlated well with photosynthetic capacity of sun-exposed foliage. However, across a broad range of plant life forms, nitrogen would be a better predictor (Field and Mooney 1986). There is evidence from field (Wessman *et al.* 1989) and laboratory studies (Card *et al.* 1988, Wessman *et al.* 1988) that foliar nitrogen concentration may be detected from reflectance signals in the short-wave infrared region. The empirical relationships from field studies are subject to the same difficulties of autocorrelation and variable background discussed in the introduction to this Chapter. Laboratory studies of dried and ground leaf material may not be transferable to whole, moist leaves. The approach of the present study, where canopy biochemistry, leaf area, and water content can be controlled independently and measured with precision, might be beneficial in future analyses of canopy biochemistry and short-wave infrared reflectance. There is much to be learned!

Table II.1. Coefficients of determination (R^2) of features from reflectance spectra *vs.* chlorophyll concentration. Sample size = 48.

	Chlorophyll Concentration	ln (1/Chl. Conc.)
Broad Band Averages		
Visible (400-700)	0.45	0.46
Blue (400-500)	0.08	0.08
Green (500-600)	0.62	0.65
Red (600-700)	0.47	0.50
Narrow Band		
565-575	0.65	0.69
1st Derivatives		
500	0.78	0.84
645	0.79	0.83
687	0.72	0.76
Other features of spectra		
Position of red edge	0.36	0.38
Distance (nm) between blue and red minima	0.81	0.85

Table II.2. Coefficients of determination (R^2) between NDVI and APAR or canopy photosynthesis when NDVI is calculated using different visible bands. NDVI was calculated from the formula (NIR-VIS)/(NIR+VIS) using the average reflectance between 800 and 900 nm for NIR and the average of the bandwidth noted for VIS. N denotes the sample size (number of canopies). R^2 values may be directly compared within columns but not across rows.

	APAR N=48	Canopy Photosynthesis (all canopies) (μmol s^{-1}) N=24	Canopy Photosynthesis (sun-exposed only) (μmol s^{-1}) N=12
VIS band width (nm)			
Visible (400-700)	0.52	0.63	0.77
Green (500-600)	0.31	0.49	0.83
Narrow Green (565-575)	0.27	0.48	0.84
Red (600-700)	0.52	0.67	0.78
Reduced Red (625-675)	0.60	0.67	0.78
Narrow Red (671-674)	0.71	0.58	0.37

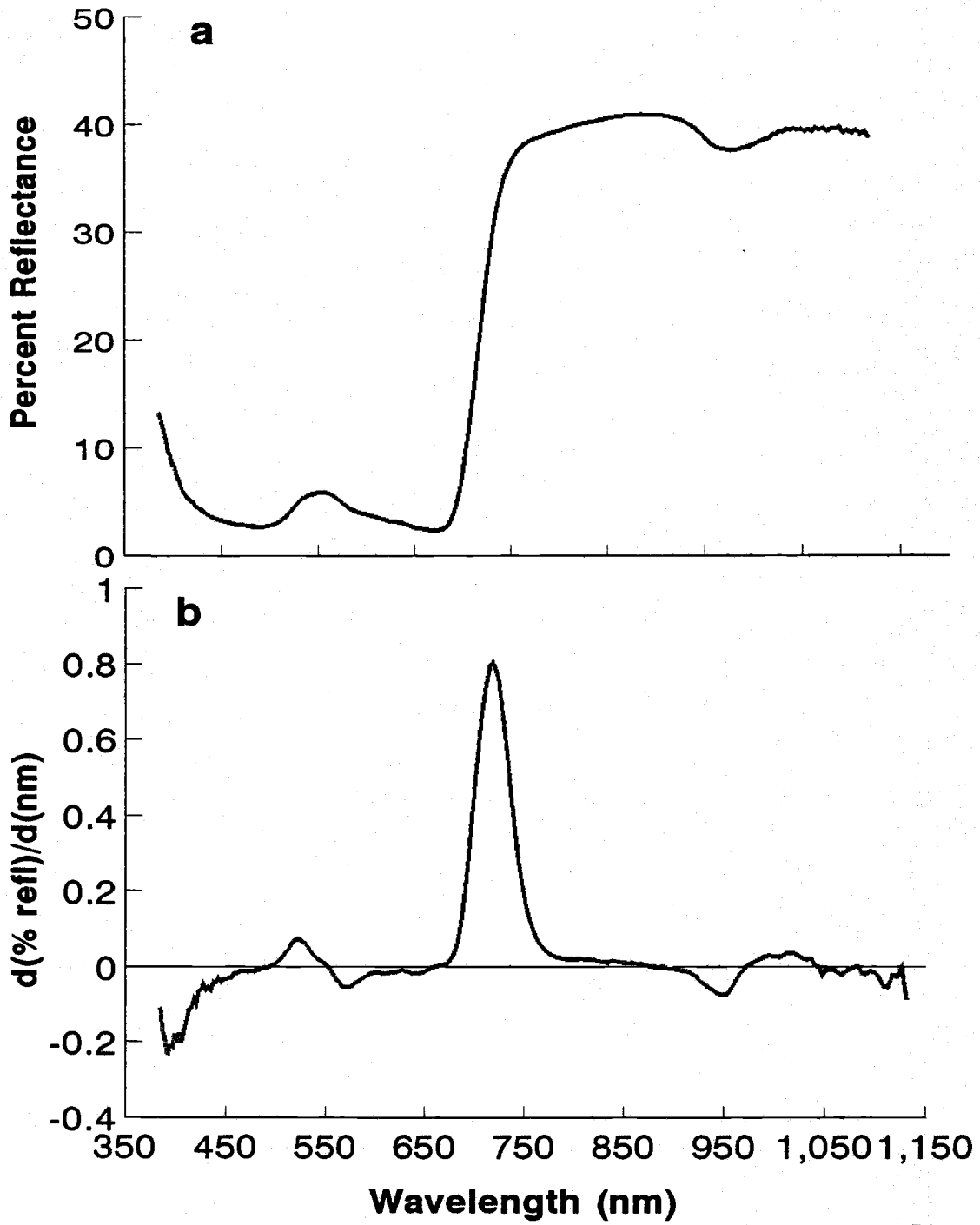

Fig. II.1. A typical reflectance spectrum (a) and 1st derivative spectrum (b) from a canopy in this study. The red edge is the rapid rise in reflectance between 650 and 750 nm. The inflection point of this edge can be located by determining the wavelength at which the 1st derivative reaches a maximum or a 2nd derivative equals zero. The first derivative was used in this study.

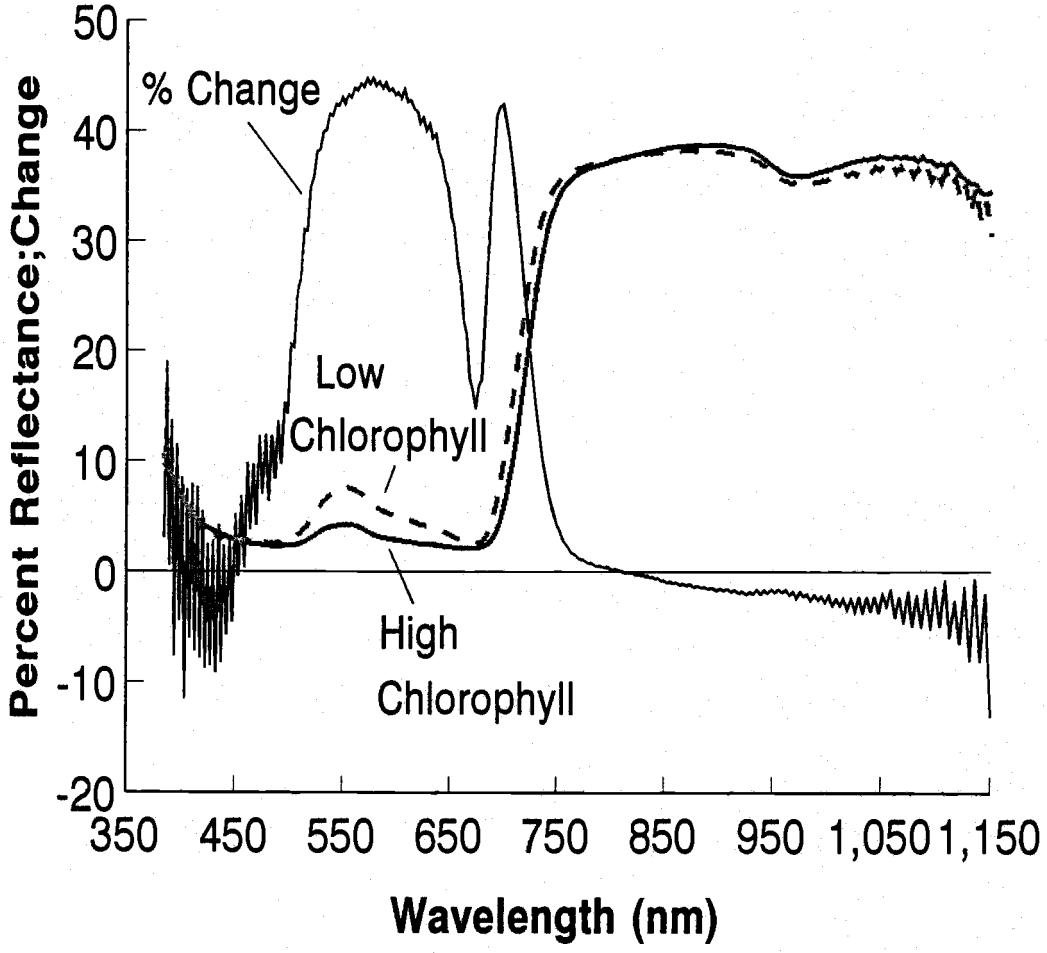

Fig. II.2. Example spectra from two canopies with nearly equal leaf area and very different chlorophyll concentrations. The percent change in reflectance of the 'low chlorophyll' canopy is referenced against the 'high chlorophyll' canopy.

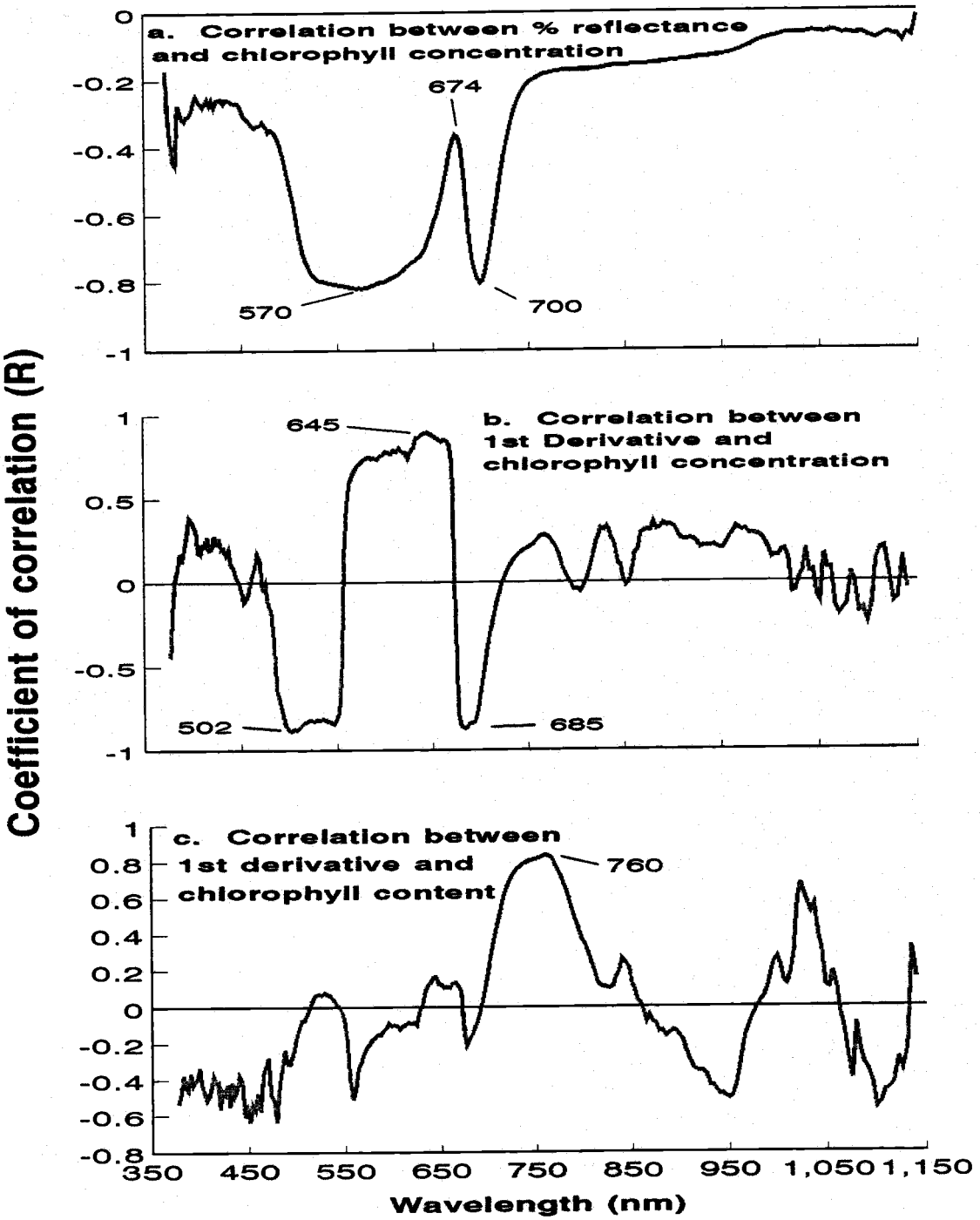

Fig. II.3. Correlelograms for chlorophyll concentration and chlorophyll content *vs.* percent reflectance and first derivatives. 'R' is the coefficient of correlation between percent reflectance (a) or the value of the 1st derivative (b,c) at each wave band and chlorophyll concentration (a,b) or chlorophyll content (c).

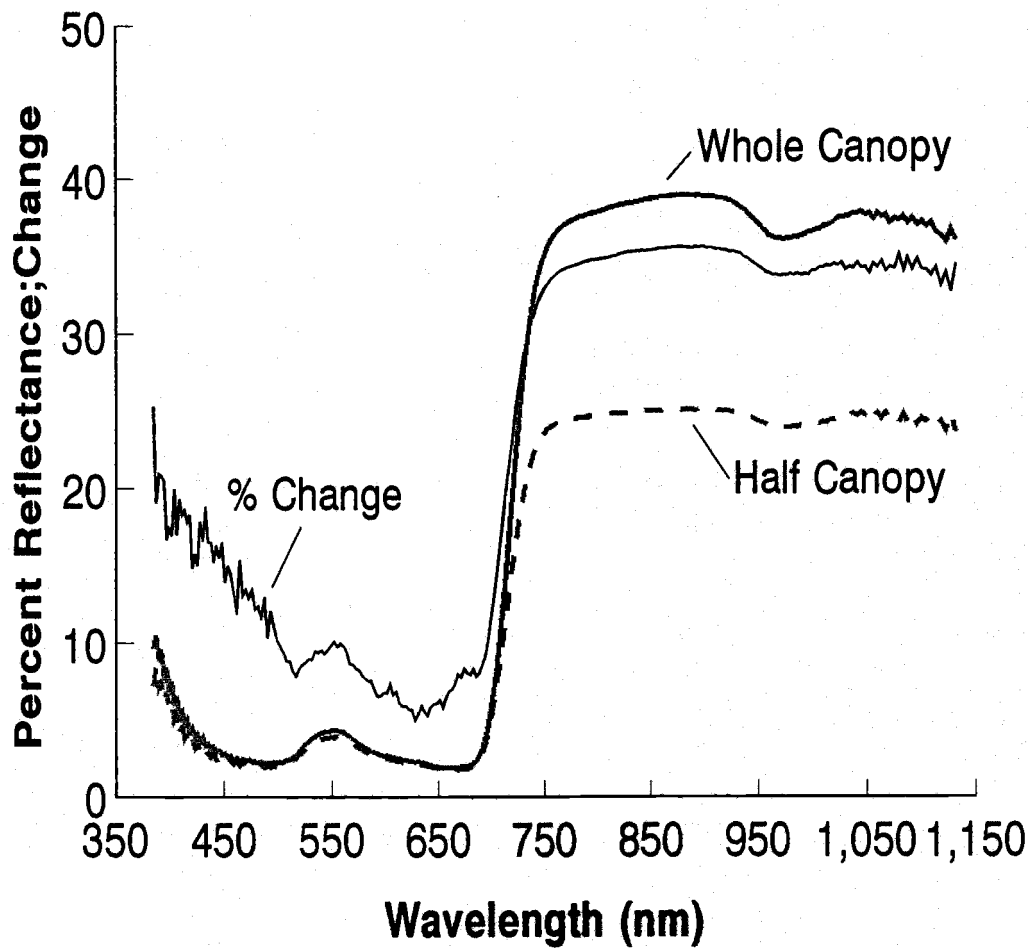

Fig. II.4. Reflectance spectra from a typical canopy with its full complement of 20 seedlings ('whole canopy') and with every other tree removed ('half canopy').

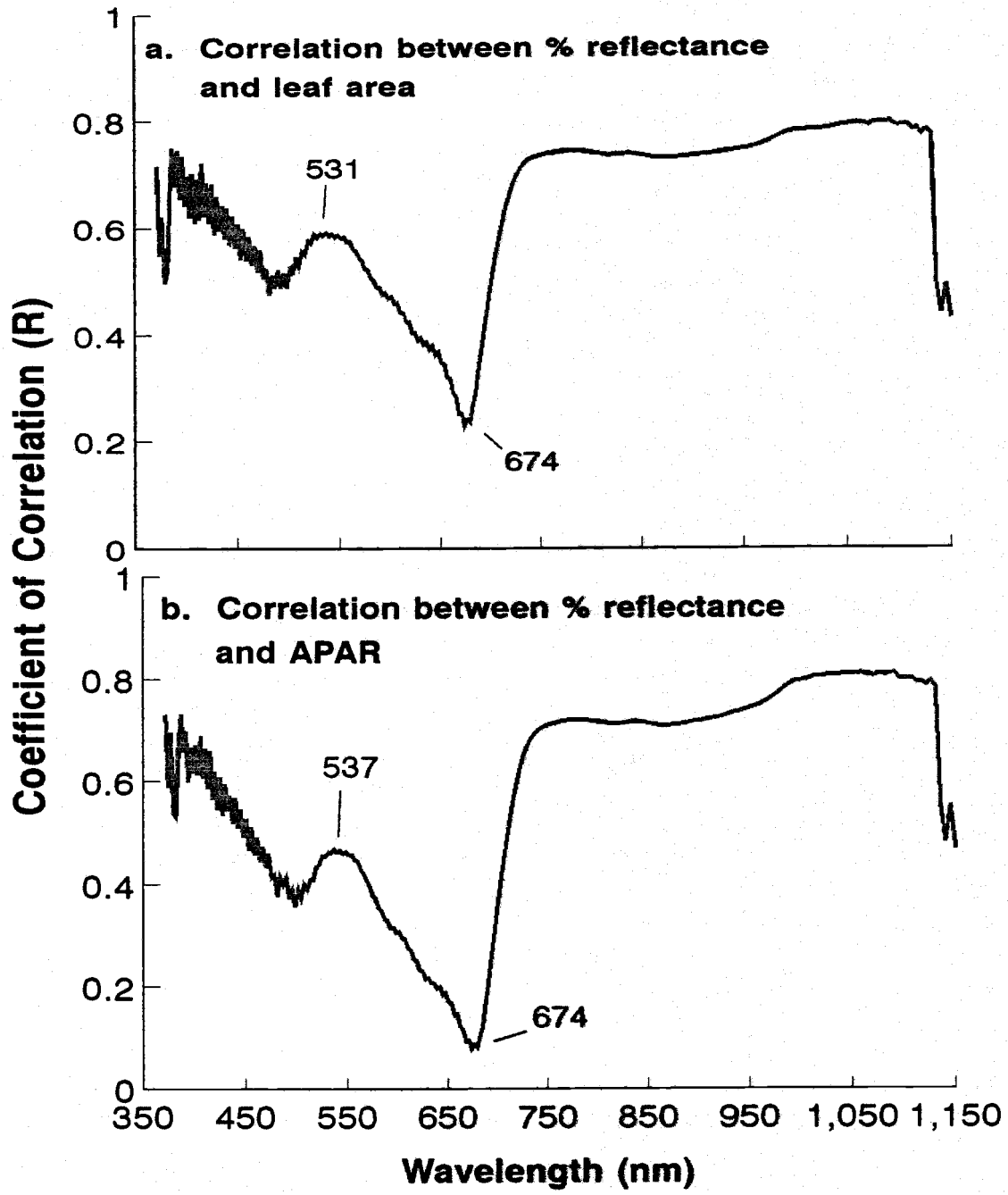

Fig. II.5. Correlelograms for leaf area and and APAR *vs.* percent reflectance. 'R' is the coefficient of correlation between percent reflectance at each wave band and leaf area (a) or APAR (b).

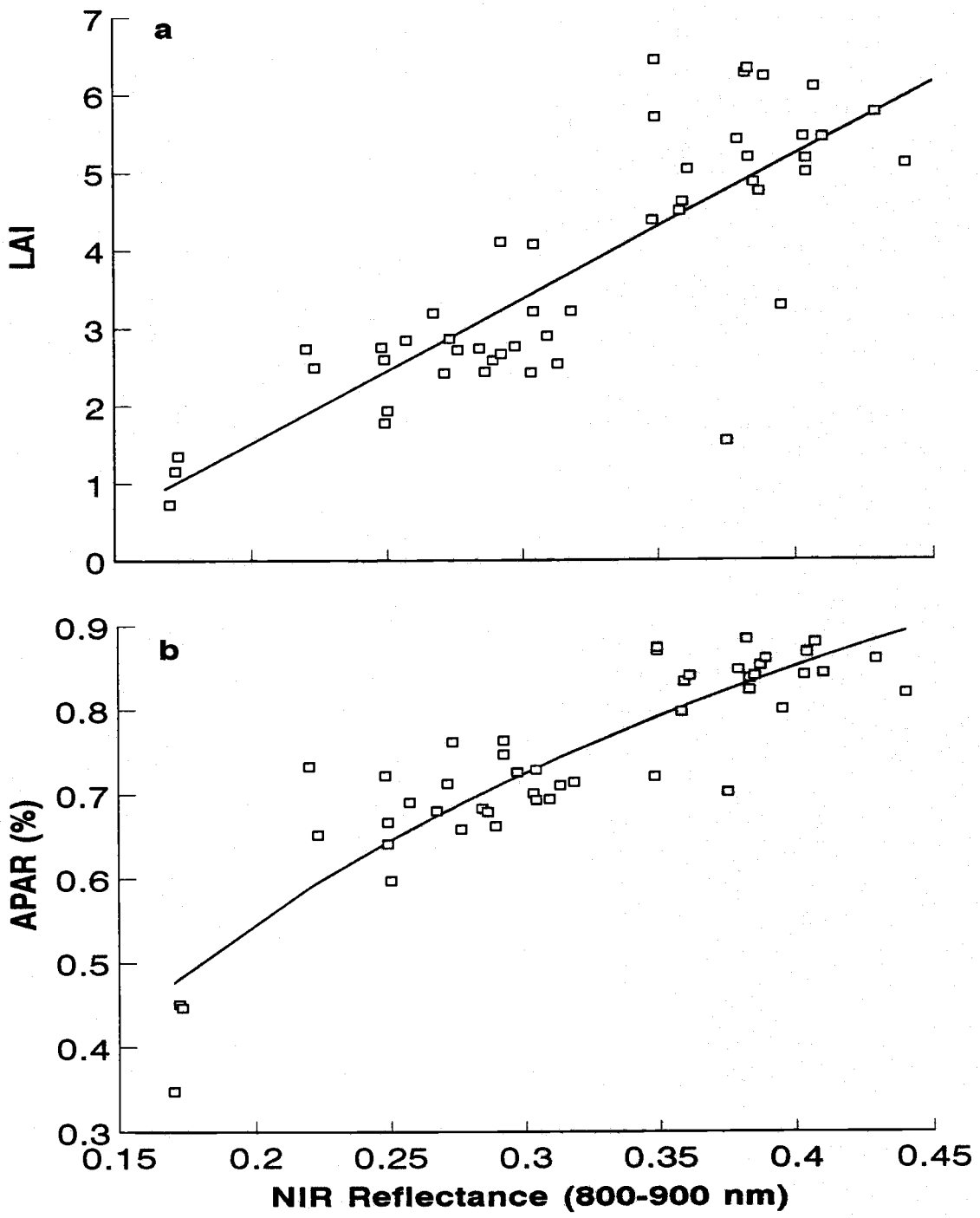

Fig. II. 6. Relationships between LAI or APAR and NIR reflectance. (a) LAI *vs.* NIR ($R^2 = 0.69$), (b) APAR *vs.* NIR reflectance ($R^2 = 0.81$)

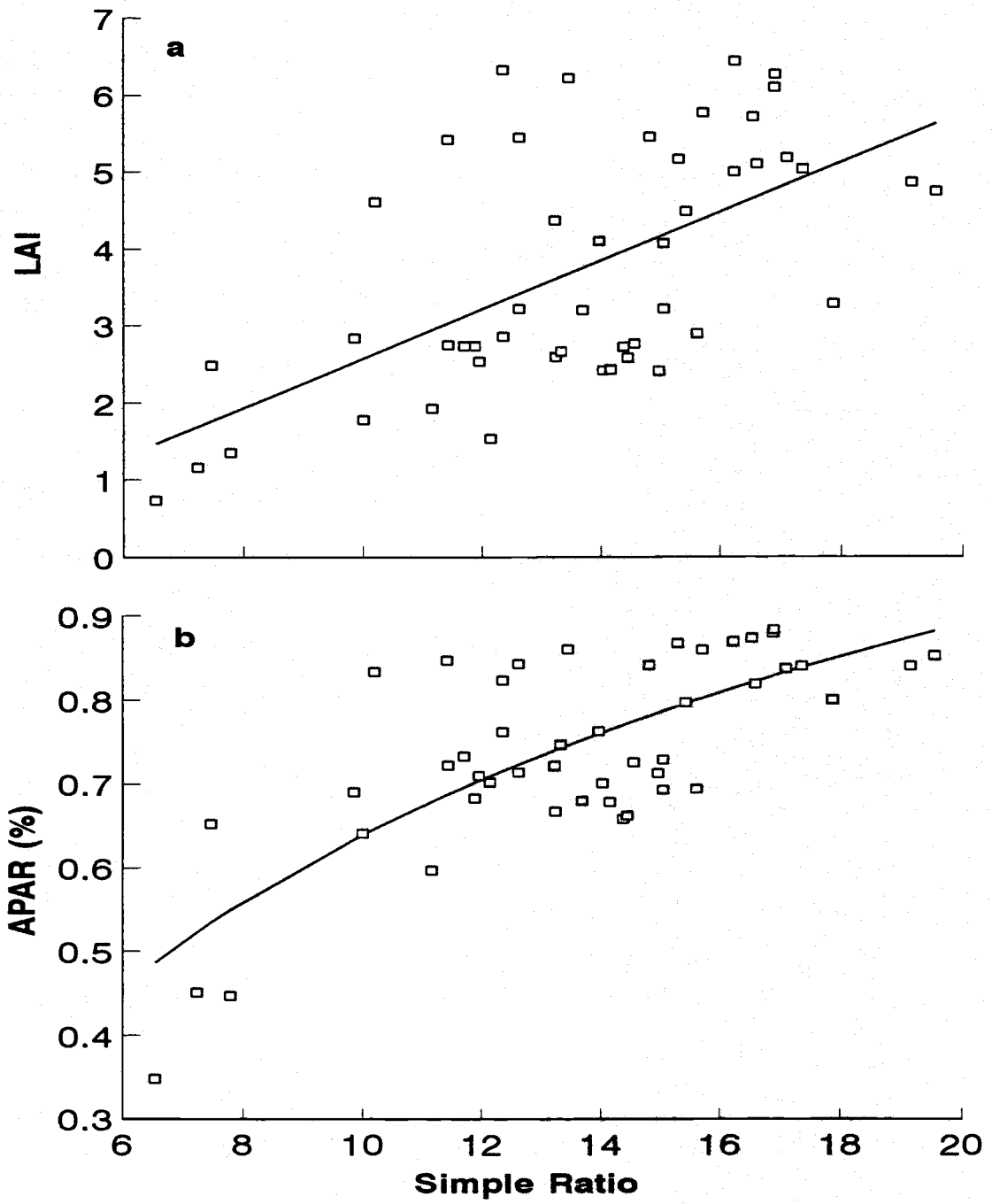

Fig. II. 7. Relationships between LAI or APAR and the Simple Ratio. (a) LAI *vs.* SR ($R^2 = 0.37$), (b) APAR *vs.* SR ($R^2 = 0.58$)

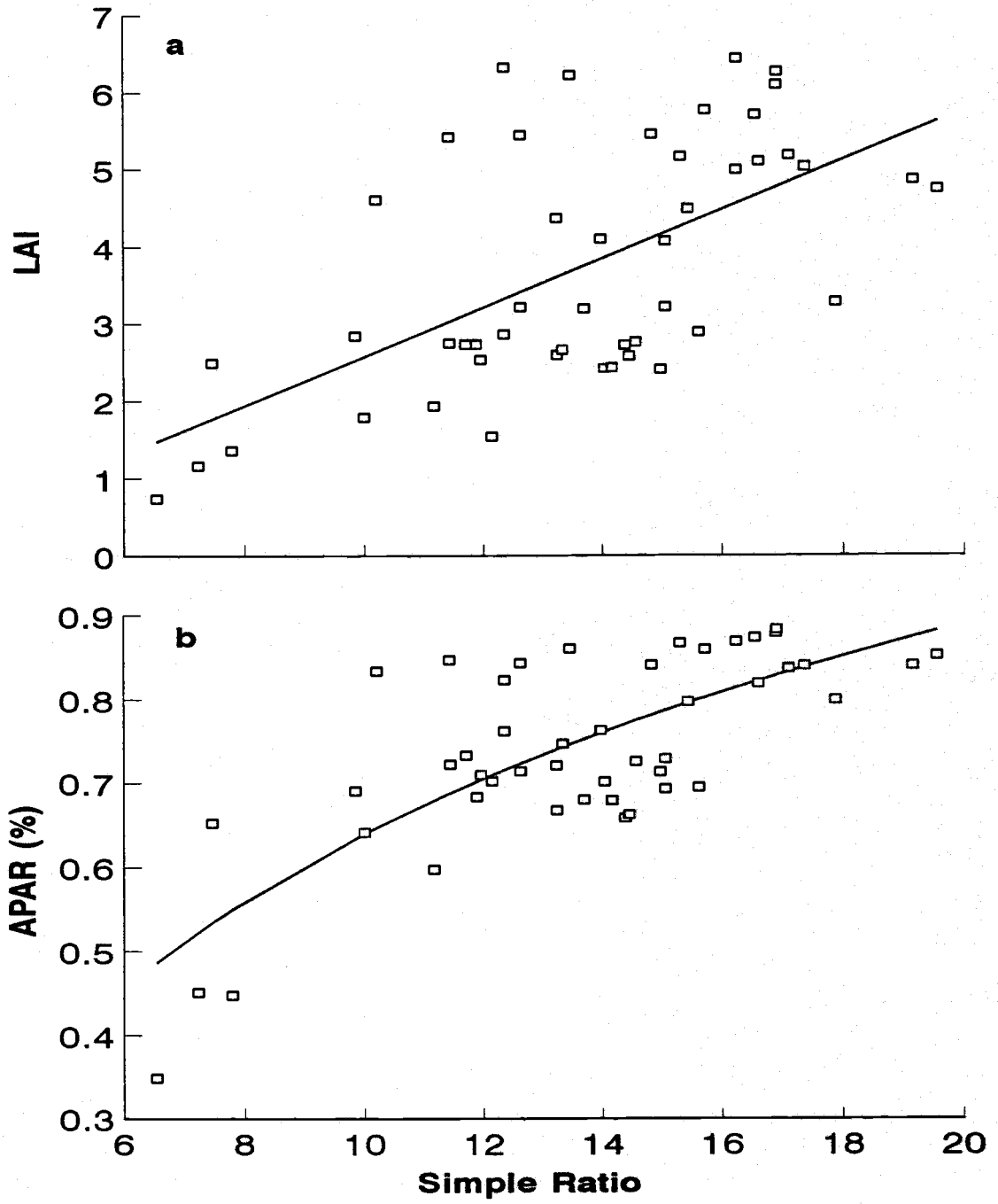

Fig. II. 8. Relationships between LAI or APAR and the Normalized Difference Vegetation Index. (a) LAI *vs.* NDVI ($R^2 = 0.36$), (b) APAR *vs.* NDVI ($R^2 = 0.60$)

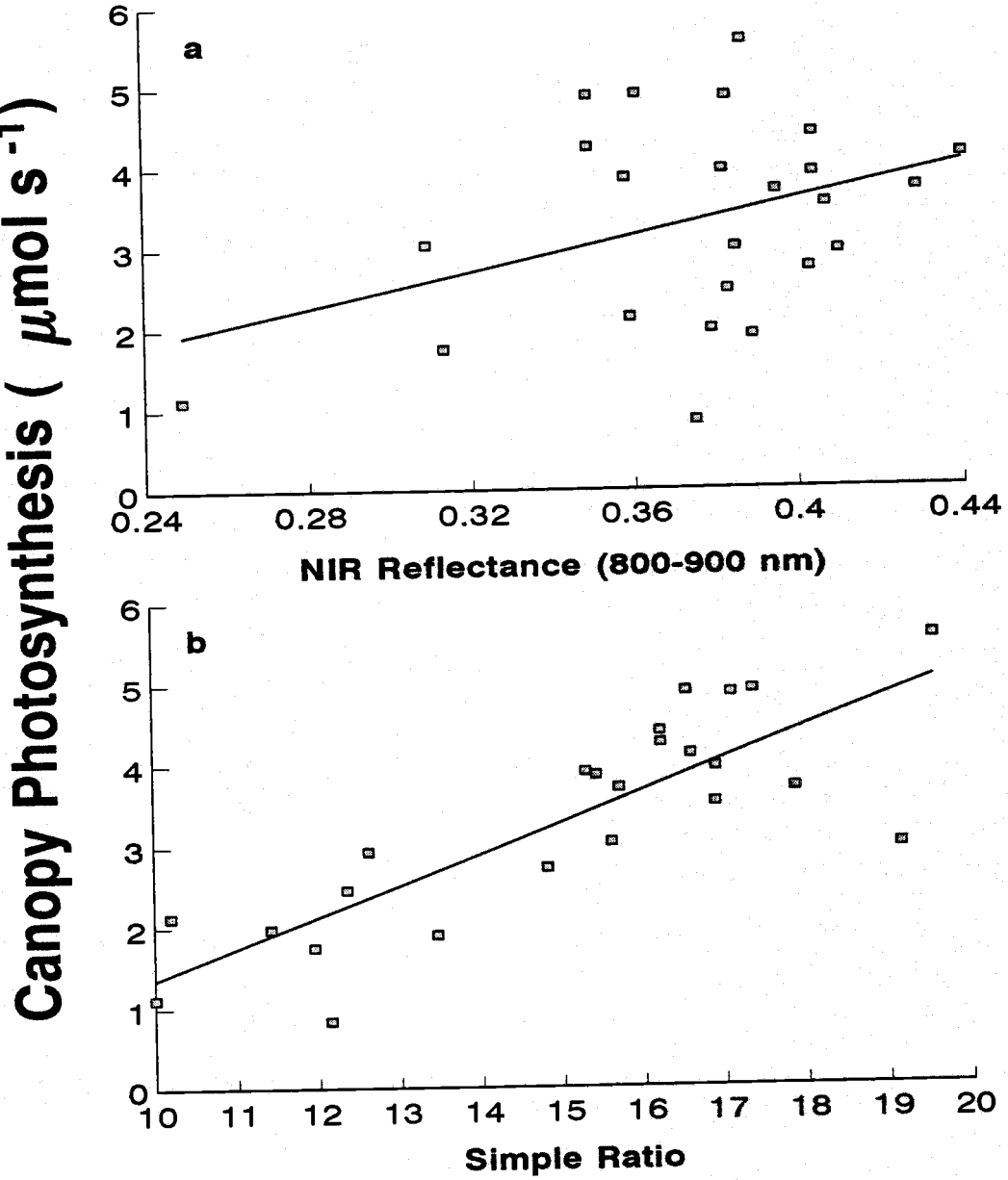

Fig. II.9. Relationships between canopy photosynthesis measured under standard conditions (photosynthetic potential) and remotely sensed indices. Because photosynthesis was measured only on whole canopies, the number of data points is half of the sample size in Figs. 6, 7, and 8 and the range of reflectance values is smaller. (a) *vs.* NIR reflectance (R^2 = 0.13), (b) *vs.* Simple Ratio (R^2 = 0.68)

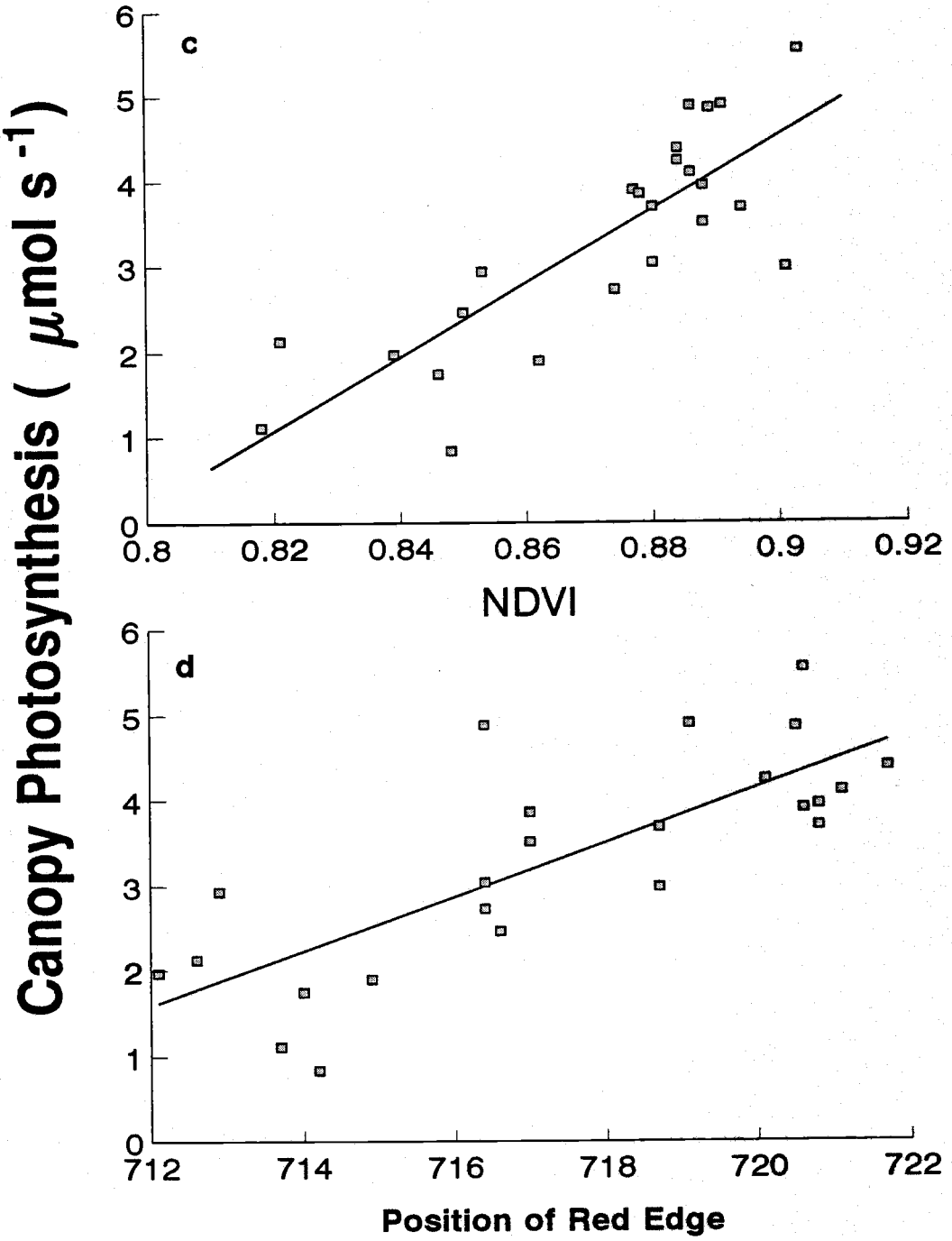

Fig. II. 9. continued. (c) *vs.* NDVI ($R^2 = 0.67$), (d) red edge ($R^2 = 0.61$).

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Chapter III

RESPONSE OF THE PHOTOSYNTHETIC CAPACITY OF MATURE WESTERN HEMLOCK TO FERTILIZATION AND SEASONAL CHANGE

ABSTRACT

I evaluated stomatal and mesophyll components of photosynthetic capacity of mature western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) in response to nitrogen fertilization through an annual cycle. There was no significant change in mesophyll capacity through the 12-month measurement period even though average daily temperatures fell below freezing during two of the collection periods. Maximum stomatal conductance was higher in the spring and fall than in the summer and winter, and this caused seasonal variation in total photosynthetic capacity.

Fertilization resulted in an average 14% increase in foliar N, but there was no significant change in mesophyll capacity with fertilization. Also there was no significant relationship between foliar nitrogen concentration and total photosynthetic capacity. It is likely that light was more limiting than nitrogen in this very dense stand, so that little of the additional nitrogen was allocated to photosynthetic enzymes. Increased maintenance respiration probably masked small increases in gross photosynthetic activity.

INTRODUCTION

The net photosynthetic activity of a plant canopy is determined by many factors. Total leaf area and photosynthetic capacity of individual leaves set an upper limit to the rate of carbon fixation, short term environmental conditions may limit photosynthetic activity to rates below the maximum, and longer term environmental conditions shape the canopy leaf area and photosynthetic capacity. Key elements required to predict canopy photosynthesis, therefore, are leaf area, unit leaf photosynthetic capacity, and environmental constraints on photosynthetic rate.

A great deal of field and laboratory research has elucidated how photosynthesis responds to short term variations in environmental factors, including light, water availability, and temperature, and this information has been incorporated into a number of process-level models of photosynthesis (examples are reviewed in Agren *et al.* 1991). Less is known about the variability of photosynthetic capacity, especially in terms of the stomatal and mesophyll components that make up total photosynthetic capacity.

In this study I evaluated the stomatal and mesophyll components of photosynthetic capacity of mature western hemlock (***Tsuga heterophylla*** (Raf.) Sarg.) in response to nitrogen fertilization through an annual cycle. A companion study (Billow *et al.* in prep.) provides information on the biochemistry of foliage from the same samples. Related studies at the same site will detail canopy leaf area and light absorption (Runyon *et al.* in prep.), litterfall, decomposition, root growth, and respiration by soils and primary producers.

My objectives in this study were three-fold. One objective was to evaluate potential seasonal change of photosynthetic capacity. Winter depression of photosynthetic capacity among temperate evergreens is well documented (e.g. Tranquillini

1957, Neilson *et al.* 1972), yet in the relatively mild climate of the Pacific Northwest conifers are believed to accumulate much of their annual carbon gain in the winter (Emmingham and Waring 1977, Waring and Franklin 1979). I hypothesized that western hemlock might have brief periods of reduced photosynthetic capacity following exposure to freezing temperatures, but that otherwise capacity should remain high throughout the winter.

My second objective was to identify relationships between leaf chemistry and photosynthetic capacity. Billow *et al.* (in prep) showed that leaf chemistry varied both in response to fertilization (foliar nitrogen increased by an average 15%) and seasonally (data are shown in Appendix I). Nitrogen concentration and photosynthetic capacity are strongly correlated in many species (Field and Mooney 1986). Because of the strong connection, nitrogen concentration has been used as an indicator of photosynthetic capacity in field research (DeJong and Doyle 1985) and ecosystem process models (Running and Coughlan 1988, Running and Gower 1991). But the correlation is weaker for evergreen shrubs and trees than it is for other species (Field and Mooney 1986, Linder and Rook 1984), especially under light-limited conditions (Rose 1989, also see Chapter 1). I asked whether the nitrogen-photosynthesis connection would hold for the very dense hemlock stand in my study. I also explored possible relationships between photosynthetic capacity and starch content of needles to determine whether high starch levels might cause feedback inhibition of photosynthetic rates.

My final objective was to determine whether possible changes in photosynthesic capacity after fertilization were be related to changes in growth of this dense stand. Most forest soils in the Pacific Northwest are nitrogen limited, and nitrogen fertilization is a common silvicultural tool. Coniferous trees typically respond to fertilization with a pulse of increased growth lasting a few years. In open stands the

growth response may result primarily from increased leaf area index (Brix and Ebell 1969, Linder and Axelsson 1982), a phenomenon that is also well known for crop plants (Watson 1952, Watson 1956). Less well understood is the response to fertilization after a stand has achieved maximum leaf area. A positive growth response in this case must either be due to an increase in photosynthetic capacity per unit leaf area, and/or a shift in allocation of photosynthate from roots to stems and shoots. Fertilization of closed stands may even reduce growth. Increased maintenance respiration will occur in tissues with higher nitrogen concentration (Ryan 1991), potentially reducing net carbon gain. I focused on possible relationships between photosynthetic capacity and growth response. Additional studies will analyze resource allocation and system carbon flux.

METHODS

Study Site

The research plots for this study were in the western Cascade Mountains near Scio, Oregon (44°40'30"N, 122°36'40"W, elevation 732 m). The forest was dominated by 30 year-old western hemlock. Snowmelt on this site usually occurs in June, with the growing season extending through October. An area encompassing the fertilized plot was given an aerial application of urea in 1988. Fertilization was repeated twice a year (spring and fall) between 1990 and 1992 with manual application of nitrogen for a total of 300 kg N per ha per year. A meteorological station was located at Roger's Mountain, 15 km west of the study site. Further details concerning the study site are in Runyon *et al.* (in prep).

Sample Collection

Samples for physiological measurements were collected from branches removed from the canopy with a shotgun. Branches were randomly selected from sunlit locations. For the 1989 collections, foliage was collected from upper canopy positions within the plots; starting in 1990, foliage was collected from trees at road edges to ensure collection of sun leaves.

On each sampling date, I obtained samples from five fertilized and five unfertilized trees. Two twigs were removed from each and the cut ends were placed in a water reservoir. They were then covered with plastic film, quickly placed in a cooler over ice, and returned to the laboratory for measurements of photosynthetic capacity. Similar foliage was harvested from each sample for biochemical analyses (Billow *et al.* in prep; Appendix). Needles formed in the previous growth year were used in all measurements. My convention was to switch to a younger cohort of needles in January.

Analysis of Growth Response to Fertilization

Growth was assessed on fertilized and control plots using cores that were taken from a random selection of 19 trees in the control stand and 18 trees in the fertilized stand. The cores were air dried, and annual growth increments were measured to the nearest 0.001 mm using a microscope. In order to distinguish between fertilizer effects and possible effects due to site differences, the growth on each plot after fertilization was analyzed relative growth on the same plot before fertilization. The average increments for 1990 and 1991 (post-fertilization) were compared with the average for 1985, 1986 and 1987 (pre-fertilization).

Measurements of Photosynthetic Capacity

In order to measure photosynthetic capacity under similar conditions throughout the year, I conducted measurements in a laboratory. I used a LiCor 6200 photosynthesis system for the gas exchange measurements. Cuvette temperature averaged 28° C during measurements and vapor pressure deficit averaged 18 mbar. These conditions were chosen because they could be maintained reliably with the measurement system. In preliminary experiments I verified that there is no significant change in photosynthesis of western hemlock immediately after cutting twigs. Because of the distance between the study site and the laboratory, our measurements were made between 12 and 24 hours after harvesting. I found that photosynthetic capacity of hemlock did decline over this period, but I was able to minimize the decline with careful handling, including a) placing samples into water reservoirs, covering with plastic, and placing over ice immediately after harvesting, b) before measurements, recutting stems under water, wiping the cut with acetone, and placing in a fresh reservoir of water before and during measurements, and c) allowing at least 20 minutes equilibration time before making measurements.

To separate the stomatal and non-stomatal components of photosynthesis, I measured 'mesophyll potential' in addition to total photosynthetic capacity. I defined mesophyll potential as the photosynthetic rate that would occur if stomatal resistance to CO_2 were zero. This is the photosynthetic rate that occurs when CO_2 concentration in the leaf mesophyll equals ambient CO_2 levels (defined at 350 $\mu l\ l^{-1}$), and is obtained by raising CO_2 external to the leaf above the ambient. I call this

measurement A_{ci350} to distinguish it from A_{ca350}, the photosynthetic rate when CO_2 external to the leaf is 350 μl l^{-1}. The value of A_{ci350} is the result of the interaction between Rubisco (ribulose bisphosphate carboxylase-oxygenase) activity and regeneration of RuBP (ribulose bisphosphate) (Farquhar *et al.* 1980). A_{ca350} is analogous to total photosynthetic capacity, although the measurement conditions were not absolutely optimal for this species.

To make these measurements, samples were removed one at a time from the cooler; a small (5-6 cm) length of stem was excised and treated as described above, then placed in a very small water reservoir sealed with a rubber gasket. The entire apparatus was then placed in a 1/4 liter cuvette. This procedure improved reliability of measurements by reducing leaks that can occur from stems crossing the foam gaskets of the cuvette. The measurement procedure requires a large differential between cuvette CO_2 and room CO_2, and I determined that even small leaks can cause significant errors. I verified through extensive tests that there was no leakage of water vapor from the reservoir. The light source was a projector bulb placed 30 cm above the cuvette, with a petri dish of water just beneath it to reduce heat load. This supplied 1600-1900 $\mu Em^{-2}s^{-1}$ PAR at the leaf surface. A fan was placed adjacent to and facing the cuvette and greatly reduced heat build up in the cuvette during measurements. Room air was humidified close to the level maintained in the cuvette, again to minimize leakage by reducing the differential of water vapor inside and outside the cuvette.

With the LiCor pump on and the system set in flow-through mode, the sample was allowed 20 to 30 minutes equilibration time with the flow rate adjusted to maintain constant vapor pressure. Then a small puff of air was introduced by mouth through a tube attached to the external flow valve to increase cuvette CO_2 to around 1200 μl l^{-1}. Photosynthesis and stomatal conductance were logged continuously with

every five μl l^{-1} change as CO_2 dropped from 1000 to 300 μl l^{-1}. A_{ci350} and A_{ca350} were determined from graphic output of the data. After gas exchange measurements, needles were removed from the twig and their projected area determined with a LiCor 3100 Leaf Area Meter. The needles were then dried at 70° C to constant weight for determination of specific leaf area (cm^2 g^{-1} dry weight).

Stomatal conductance varied slightly during the course of measuring photosynthesis on each sample. In general, conductance increased as CO_2 in the cuvette decreased. The values reported are for the conductance that occurred when cuvette CO_2 was 350 μl l^{-1}, or at the same point that A_{ca350} values were recorded. In approximately 10% of the samples, stomata never opened enough for reliable measurements. These were eliminated from the data set.

Field Measurements of Photosynthesis

Photosynthesis was measured at the study site to assess differences between fresh-cut samples and samples that were returned to the laboratory. Samples of sunlit foliage were collected by shotgun and immediately placed in the 1/4 l cuvette. Measurements were made in full sun (greater than 1000 μE m^{-2} s^{-1}) and completed within 3 minutes of harvesting.

Statistical Analyses

The fertilization and sampling date effects were analyzed by Analysis of Variance. There were 21 degrees of freedom in the model, one for fertilization treatment, ten for sampling date, and ten for their interaction. Because of missing observations I used the Least Squares Means routine of a General Linear Models

Procedure to obtain maximum likelihood means and standard errors (SAS Institute 1985). Pairwise comparisons were made among means using the conservative Bonferroni test (Neter and Wasserman 1974) with $\alpha = 0.05$.

I used least squares regression to determine relationships between leaf chemistry and photosynthetic capacity. A T-test was used to evaluate growth effects.

RESULTS

Climatic Conditions

The climate at the study site during the measurement year was typical for this region (Fig. III.1), with cool, moist conditions during the winter and warm, dry conditions during the summer. Mean daily temperatures were below freezing during the December sampling and near freezing during the January sampling; minimum temperatures (not shown) were well below freezing at both times. Although precipitation was low during the summer, drought conditions here were not as severe as in many other parts of western Oregon. Pre-dawn xylem potential was never measured below - 0.65 MPa.

Photosynthetic Responses to Fertilization and Seasonal Change

Results of the physiological measurements are summarized in Fig III.2. A_{ca350} averaged 3.4 μmol m^{-2} s^{-1} overall, with the highest monthly means approaching 5 μmol m^{-2} s^{-1}. This is less than the maximum photosynthetic rates I measured in the field (Table III.1). The difference is probably a consequence of partial stomatal closure in the laboratory, as discussed in METHODS.

Table III.1. Field measurements of photosynthesis (μmol m^{-2} s^{-1}) on current and one-year-old foliage, July 26, 1991. N = 3; standard errors are in parentheses. There were no significant differences due to needle age or fertilization treatment.

	Current foliage	One-year-old foliage
Control	5.2 (0.4)	6.9 (0.2)
Fertilized	4.9 (0.7)	5.6 (0.3)

There was no statistically significant variation in A_{ci350} due to either sampling date or fertilization. Interestingly, the lowest A_{ci350} values occurred in March rather than during the months of greater extremes of climate. Seasonal variation was significant for A_{ca350} and is somewhat bimodal, with lowest values in the winter summer, and highest values in the spring and fall. Since A_{ci350} did not vary seasonally, the change in A_{ca350} is the result of changes in stomatal conductance, which were strongly bimodal through the annual measurement course.

Mean values of A_{ci350}, A_{ca350} and stomatal conductance measured in the laboratory as well as field photosynthesis were actually lower for foliage from fertilized trees. In the case of A_{ca350} the decrease is statistically significant (Fig. III.3). When the data are analyzed as a function of leaf nitrogen rather than fertilization treatment, however (Fig. II.5), no significant relationship is apparent between nitrogen and photosynthetic capacity across the data set.

Growth Response to Fertilization

The radial stem growth on both control plots and fertilized plots was significantly lower after fertilization ($p < 0.05$) (Table III.2). The change is probably a result of less favorable environmental conditions during the two years after fertilizer application was initiated. There was no significant difference between fertilized and control treatments in either absolute or relative growth increments.

Table III.2. Growth of annual rings before fertilization treatment (1985-1987) and after (1990-1991). 'Relative Growth Response' is the average increment after fertilization divided by the average increment before fertilization. Standard errors are in parentheses.

	Average Annual Increment (mm)		Relative Growth Response
	1985-1987	1980-1991	
Control (N=19)	2.0 (0.2)	1.6 (0.1)	0.81 (0.07)
Fertilized (N=18)	2.1 (0.2)	1.7 (0.2)	0.84 (0.06)

DISCUSSION

Seasonal Change

Winter depression of photosynthetic capacity among temperate evergreens is well documented and often associated with frost hardiness (e.g. Tranquillini 1957,

Pharis *et al.* 1970, Neilson *et al.* 1972) and a decline in chlorophyll concentrations (Linder 1980). The reduced photosynthetic capacity has been related to a variety of changes to the leaf mesophyll, including reduced enzyme levels (Gezelius and Hallen 1980) and reduced fluorescence yield (e.g. Hawkins and Lister 1985, Krause and Somersalo 1989). Decreased photochemical activity probably protects foliage from photodamage by reactive oxygen species produced when very cold temperatures limit the biochemical reactions of photosynthesis. The western hemlock in this study, however, showed no significant change in A_{ci350} through the winter months. This was despite the fact that temperatures at the study site fell well below freezing during the December and January collection periods.

In controlled environment studies, seedlings of western hemlock have been shown to harden to frost, but the hardening process is independent of entry into dormancy, and maximum degree of hardiness is less than many other western conifers, including noble fir and ponderosa pine (Timmis 1976). Reports of absolute minimum temperature vary. Fowells (1965) reported a minimum temperature range between -6.7° C to -28.9° C for coastal western hemlock, while trees from Alaska and British Columbia reportedly have much lower absolute temperature minima (Krajina 1969, Watson *et al.* 1971). But in general the range of western hemlock is restricted to moderate temperatures. It appears that this species maintains constant mesophyll capacity for photosynthesis through occasional freezing spells and is therefore in a position to photosynthesize at high rates during intermittent warm periods. These results are consistent with the suggestion that as much as 50% of the annual net carbon gain of some western conifers may occur in the winter months (Emmingham and Waring 1977). Waring and Franklin (1979) suggested that the dominance of conifers in the Pacific Northwest is in part a consequence of wintertime photosynthesis due to moderate temperatures in the area. Another factor may be the persistent

cloud cover during the winter, because the trade off for maintaining high mesophyll capacity is probably a high sensitivity to photodamage during very cold periods.

Mean values of A_{ci350} were lower in March that at any other time of the year. Although the decrease was not significant statistically in my sampling, it may be an indication of real variation. Fry and Phillips (1977) also noted a pronounced decline in photosynthetic capacity of three conifers, including western hemlock, before bud break. In my study the decline corresponded to changes in leaf chemistry: both chlorophyll and amino acids were at a minimum in March (Billow *et al.* in prep, Appendix). It is likely that there is a large shift nitrogen pools at this time, in preparation for bud break. Although nitrogen apparently is not limiting at this site (Billow *et al.* in prep., also see below), a mobilization among pools may cause a temporary reduction in rubisco levels, and a consequent drop in mesophyll potential. A_{ci350} did not change in response to very high starch concentrations in May and June (Appendix), confirming earlier studies on conifers demonstrating that photosynthesis is not influenced by end-product accumulation (Little and Loach 1972).

Effects of Fertilization

A strong correlation between leaf nitrogen concentration and photosynthetic capacity has been reported for many species, but for the western hemlock in this study, photosynthetic capacity was generally independent of leaf nitrogen. In general the nitrogen-photosynthesis connection is weaker for evergreen trees and shrubs than it is in other species (Field and Mooney 1986, Linder and Rook 1984). An often-cited figure in Field and Mooney (1986) shows good correlation between nitrogen and photosynthetic capacity across a broad range of vegetation types, but the evergreen sclerophylls are clumped together. When the evergreen sclerophylls are viewed as an

isolated group, their nitrogen-photosynthesis correlation is low.

Additional information helps explain the results from the present study. The nitrogen concentration of foliage from unfertilized trees, which averaged 1.3% by weight (Appendix) was near the maximum reported for western hemlock seedlings (1.4%-1.6%; Radwan and DeBell 1980). This, along with the large increase in the concentration of free amino acids in foliage from fertilized trees (Appendix), suggests that nitrogen probably was not limiting on this site (Appendix). Other environmental factors probably limited photosynthetic activity, so little of the increased leaf nitrogen was allocated to Rubisco and other carbon fixing enzymes. The most likely limiting factor is light. Foliage was collected from sun-exposed sides of trees, but in these tall, dense canopies even those areas probably received only a few hours of direct sun each day.

Increased maintenance respiration may partially explain the observed results. Maintenance respiration increases as the nitrogen concentration of a tissue increases (Ryan 1991). In a related study, dark respiration was measured *in situ* on foliage in the control and fertilized plots studied here. Dark respiration was up to 35% higher on the fertilized plots (M.G. Ryan, unpublished data). It is likely that there was a small increase in gross photosynthesis in response to fertilization, but this was masked by the increase in dark respiration.

Other nutrients, especially phosphorus, are potential candidates as limiting factors. Phosphorus content was significantly lower in foliage from fertilized trees (Appendix). This result concords with previous research on western hemlock demonstrating that nitrogen fertilization reduces phosphorus concentration (Gill and Lavender 1983a,b), possibly by affecting root mycorrhizae (Gill and Lavender 1983b) or because of a dilution effect caused by increased total leaf growth. The relative proportions of nitrogen and phosphorus shifted from an average 100:12 for control

foliage to 100:8 for fertilized foliage. Both values are lower than the optimal N:P proportion for western hemlock (100:16; Van den Burg 1979, reported in Ingestad 1979), but phosphorus concentration was always greater than 0.1% by weight. It is unlikely that phosphorus depletion affected photosynthetic activity.

Fertilization, Photosynthetic Capacity and Growth

Previous studies have shown that western hemlock has a varied response to fertilization (Radwan and DeBell 1980); nitrogen fertilization may even result in reduced growth. In this study, the fertilizer caused no change in stem growth. Leaf area index was the same in fertilized and control treatments, near 10 $m^2 m^{-2}$ (Runyon *et al.* in prep), and leaf production was probably the same because there were no differences in litterfall in fertilized and unfertilized plots (Myrold and Claycomb, unpublished data). Total canopy photosynthesis must have also been similar on fertilized and unfertilized plots, since there was no significant change in photosynthetic capacity.

In summary, heavy application of nitrogen fertilizer resulted in significant changes to foliar chemistry (Billow *et al.* in prep, Appendix), but no change to net canopy photosynthesis or stem growth. Very dense stands such as the hemlock in this study may be more limited by availability of light than by other resources.

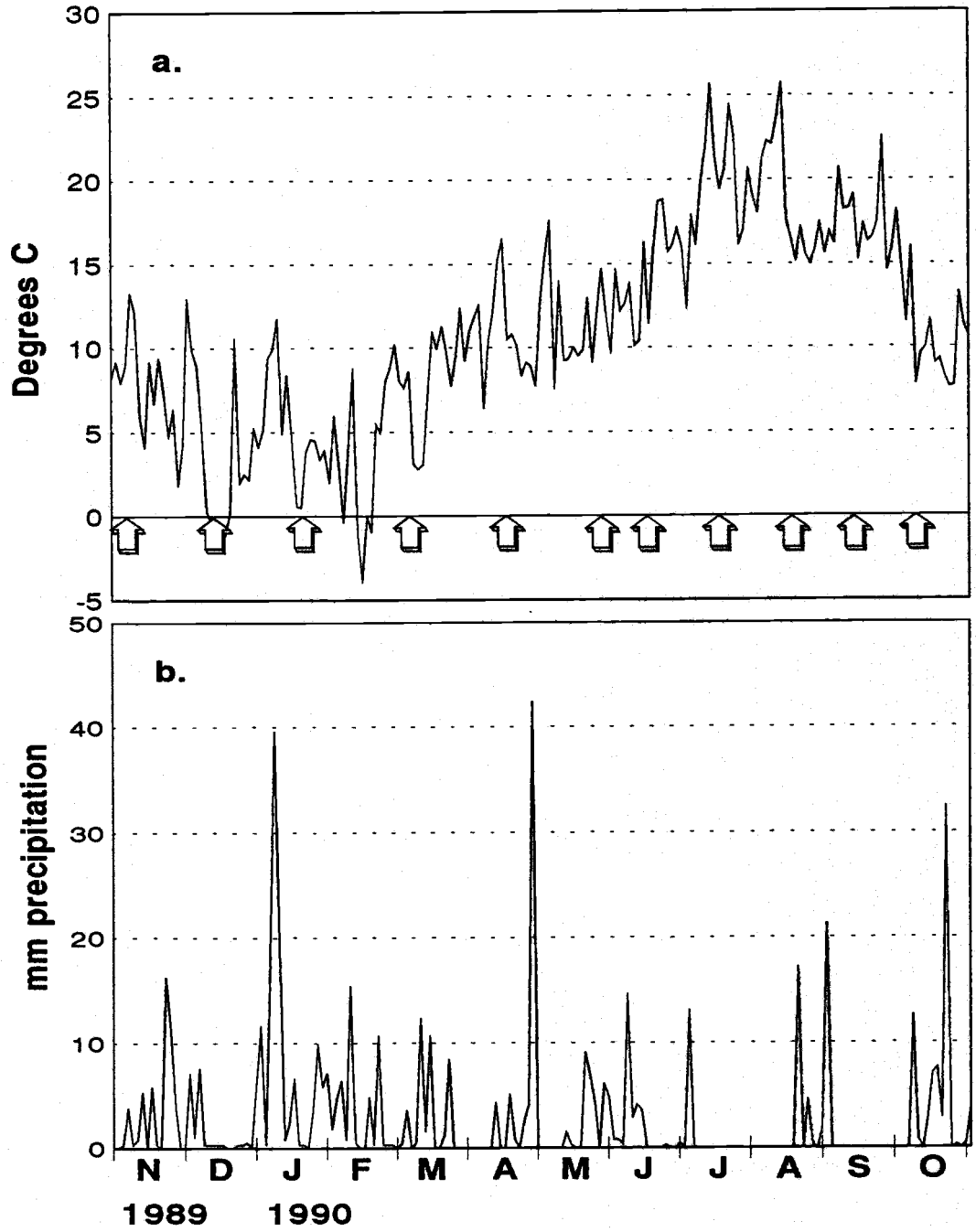

Fig. III.1. Climate conditions at the Scio study site during the course of physiological measurements. a) Mean daily temperature, b) Total daily precipitation. Collection dates are noted with arrows in **a**.

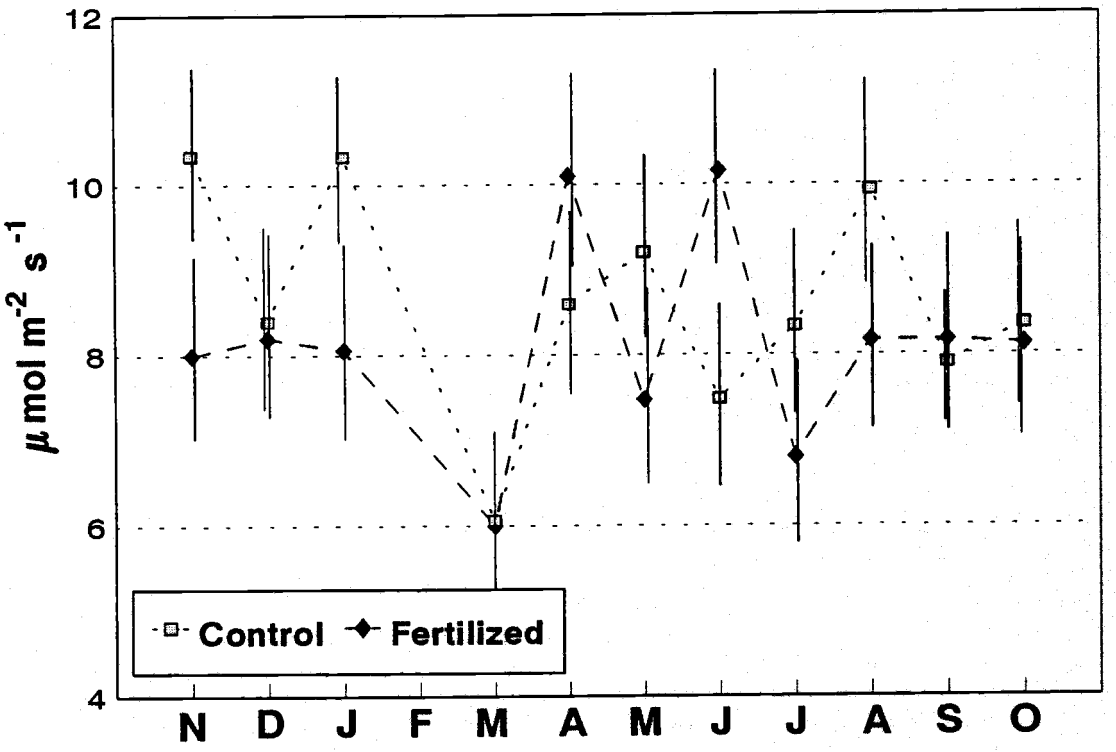

Fig. III.2. Mesophyll capacity (A_{ci350}) of foliage from fertilized and unfertilized trees through the 1-year measurement cycle. Vertical bars indicate pooled standard errors adjusted for sample size, which varied from 3 to 5. Analysis of variance indicated no significant differences by sampling date, fertilization treatment, or their interaction.

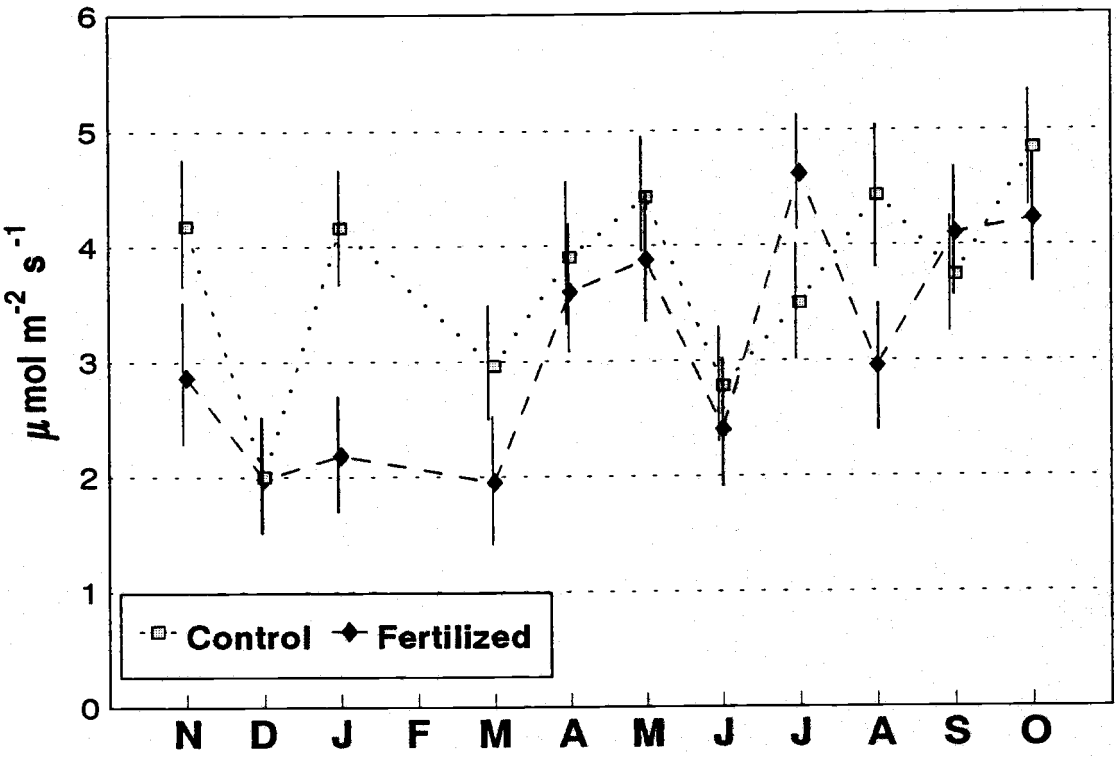

Fig. III.3. Total photosynthetic capacity (A_{ca350}) of foliage from fertilized and unfertilized trees through the 1-year measurement cycle. Vertical bars indicate pooled standard errors adjusted for sample size, which varied from 3 to 5. Analysis of variance indicated significant differences due to both fertilization ($P < 0.029$) and sampling date ($P < 0.0001$), with no significant interaction. The overall mean for fertilized foliage (3.15) was less than for control foliage (3.71). In general the photosynthetic capacity was highest in the fall and spring. Significant differences from pairwise comparisons using the Bonferroni test ($\alpha = 0.05$) included: Dec. *vs.* May, July, Sept., Oct.; March *vs.* Oct.; June *vs.* Oct.

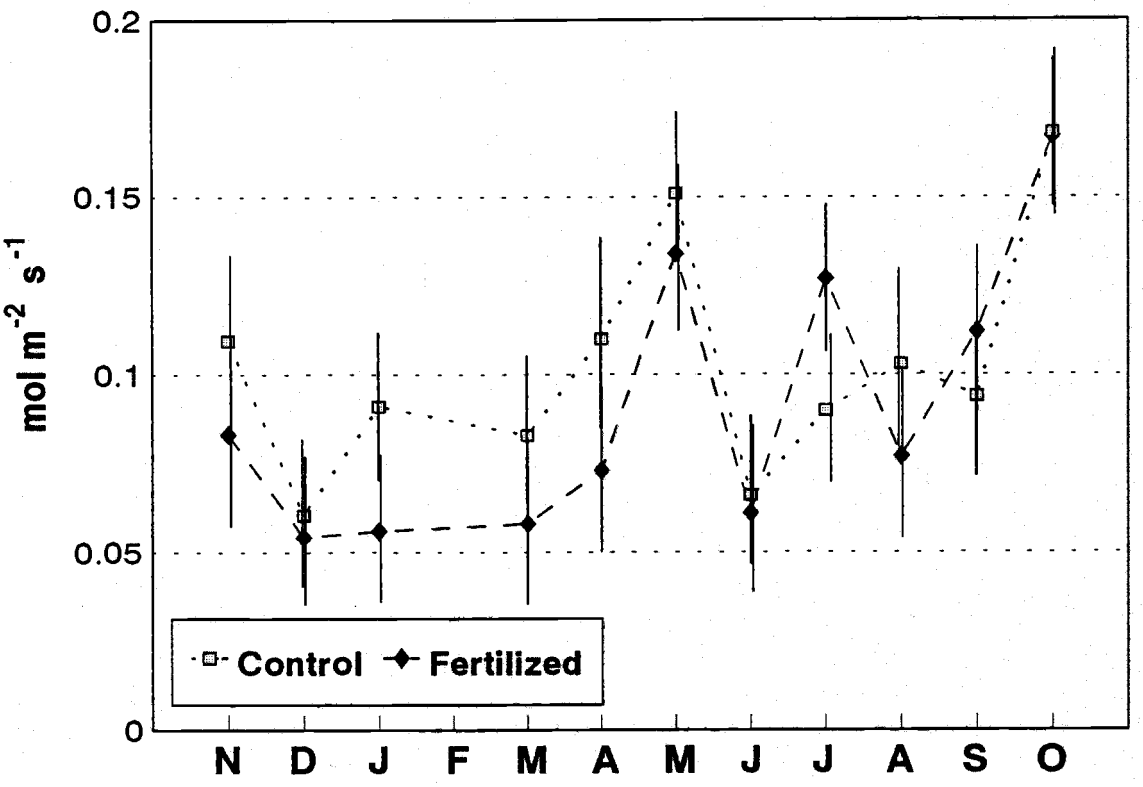

Fig. III.4. Stomatal conductance measured under standard conditions of foliage from fertilized and unfertilized foliage through the 1-year measurement cycle. Vertical bars indicate pooled standard errors adjusted for sample size, which varied from 3 to 5. Analysis of variance indicated no significant differences due to fertilization, although differences due to sampling date were significant ($P<0.0001$). There was no significant interaction. In general the stomatal conductance was highest in the fall and spring. Significant differences from pairwise comparisons using the Bonferroni test ($\alpha=0.05$) included: Dec. *vs.* May, Oct.; June *vs.* May, Oct.; Jan. *vs.* Oct.; Mar. *vs.* Oct.

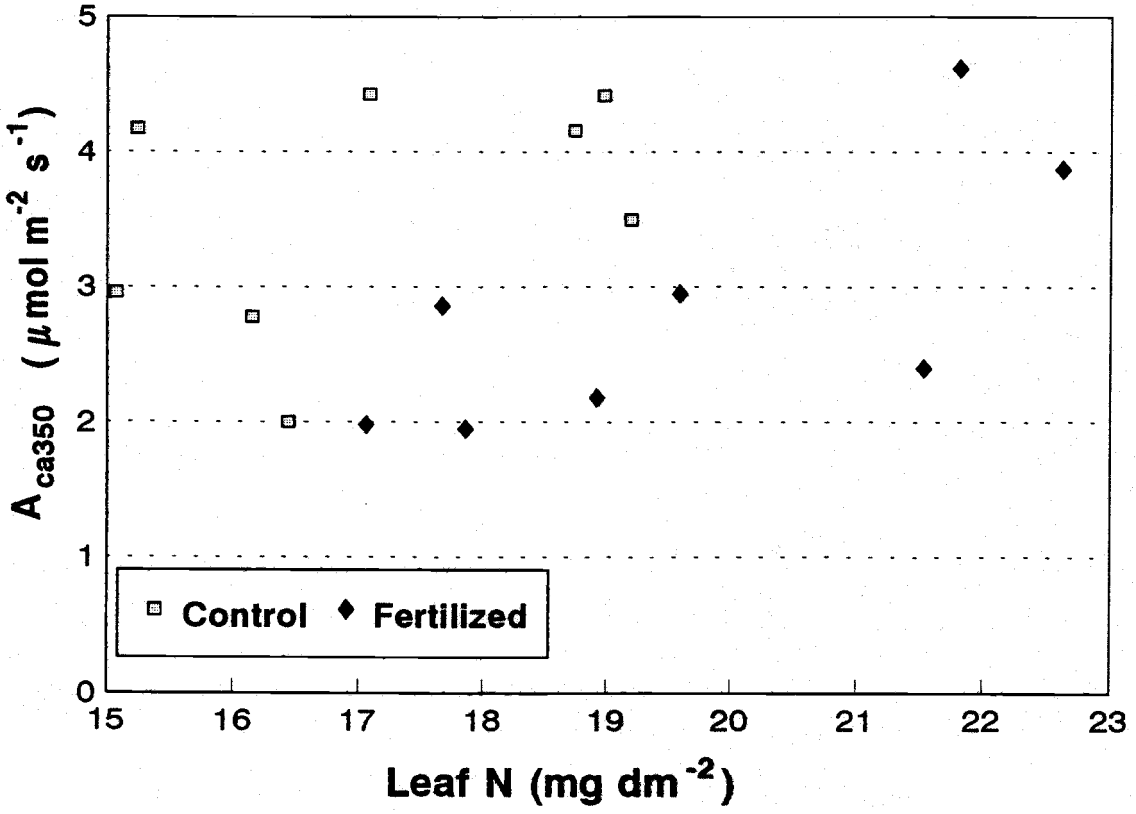

Fig. III.5. Relationships between mean values of total photosynthetic capacity and leaf nitrogen concentration for each sampling period. Some of the data shown in Fig. II.3 are not shown here because leaf chemical analyses were not performed on some collection dates. For all data points combined and for the control data points, there is no relationship between leaf N and photosynthetic capacity (slope is not significantly different from zero). There is a significant positive trend for the foliage from fertilized trees ($P < 0.01$).

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APPENDIX

APPENDIX: Chemical composition and specific leaf area of western hemlock leaf tissue used for physiological analyses in Chapter 3. These data are presented separately because they will be published as a separate paper (Billow *et al.*, in prep). The leaf tissue for chemical analyses was collected simultaneously with the samples for the physiological measurements (some details are in Chapter 3, more are in Billow *et al.*, in prep). The chemical analyses were performed at the Ames Research Center, Moffet Field, CA, by C.R. Billow. Specific leaf area was determined at Oregon State University by B.J. Yoder using the needles that were used in physiological measurements. Statistical summaries are based on ANOVA analysis as described in Chapter 3, with $\alpha=0.05$.

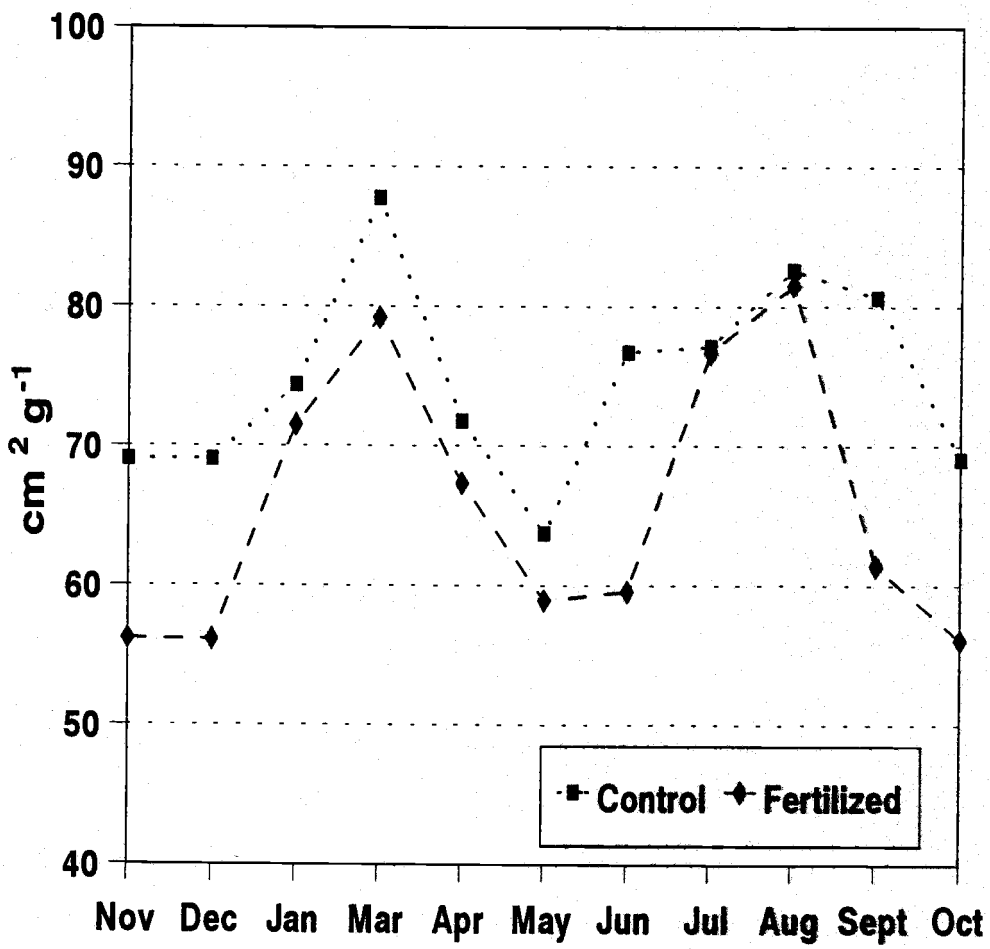

Fig. A.1. Specific leaf area of foliage from fertilized and unfertilized western hemlock through a 1-year measurement cycle. Differences due to fertilization were not statistically significant. Differences due to sampling date and interaction effects were significant.

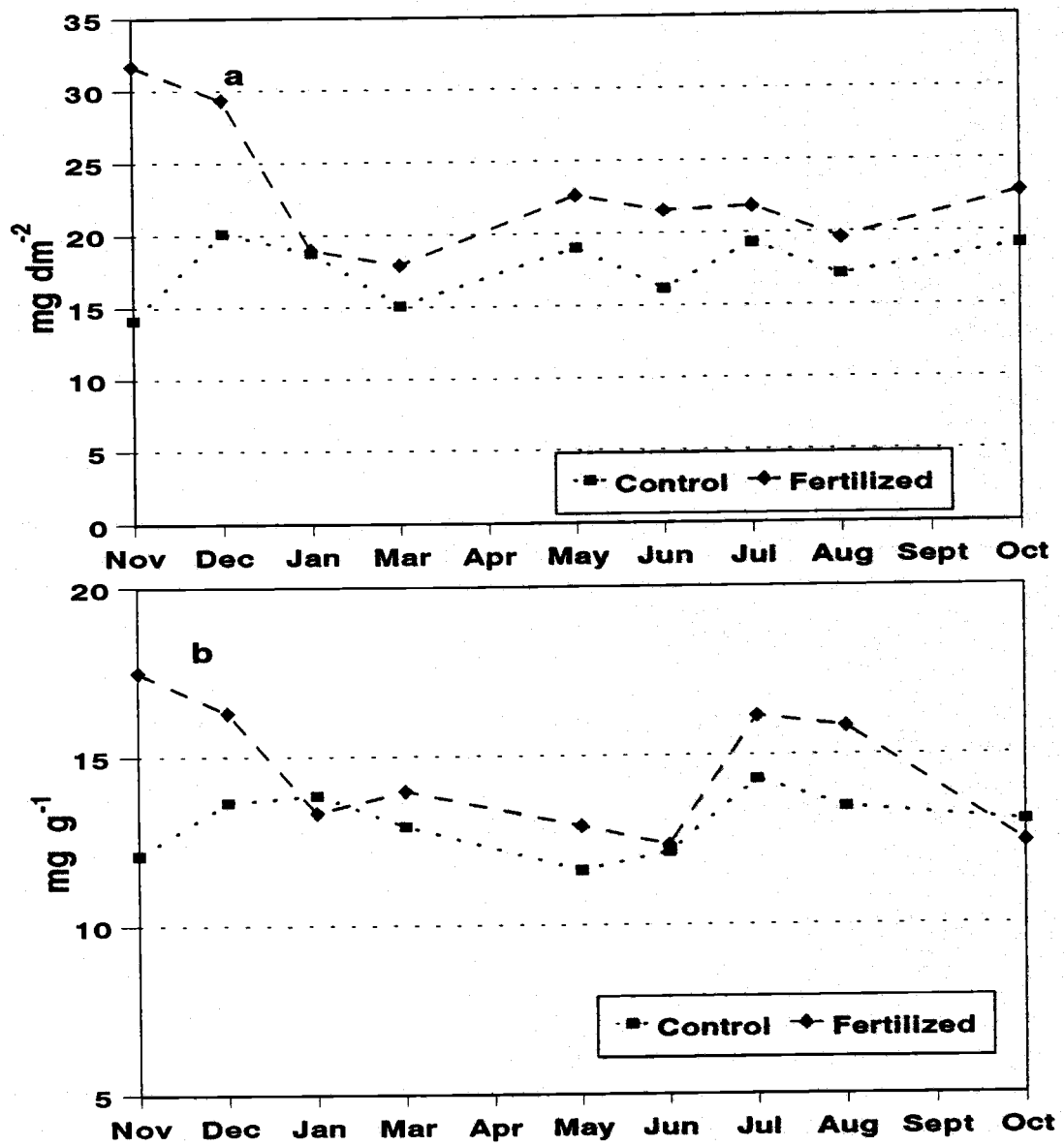

Fig. A.2. Nitrogen concentration of foliage from fertilized and unfertilized western hemlock through a 1-year measurement cycle. a) by unit area, b) by unit weight. Differences in a were significant with fertilization treatment, but not with sampling date or interaction effects.

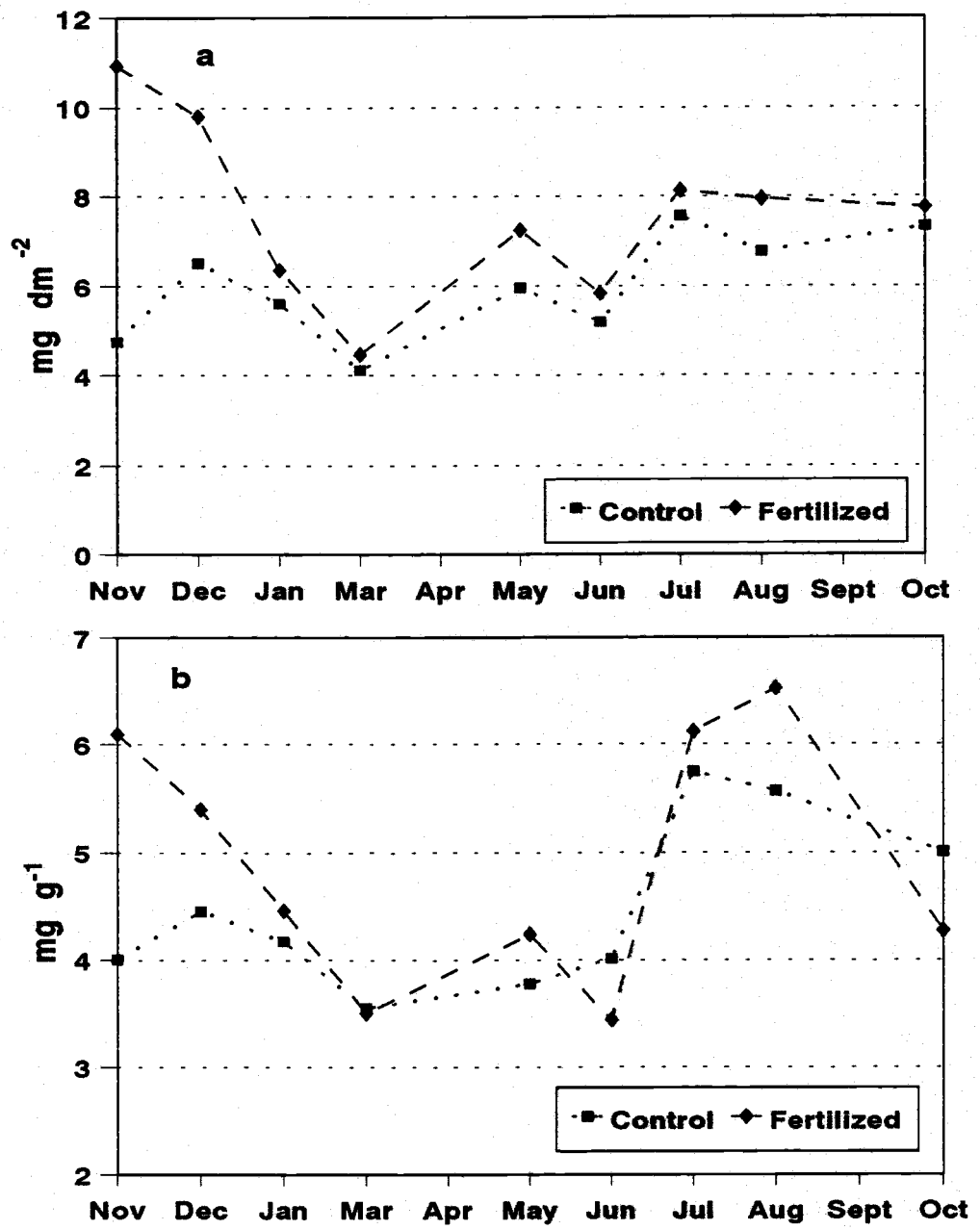

Fig. A.3. Chlorophyll concentration of foliage from fertilized and unfertilized western hemlock through a 1-year measurement cycle. a) by unit area, b) by unit weight. Differences in a were significant with fertilization treatment, but not with sampling date or interaction effects.

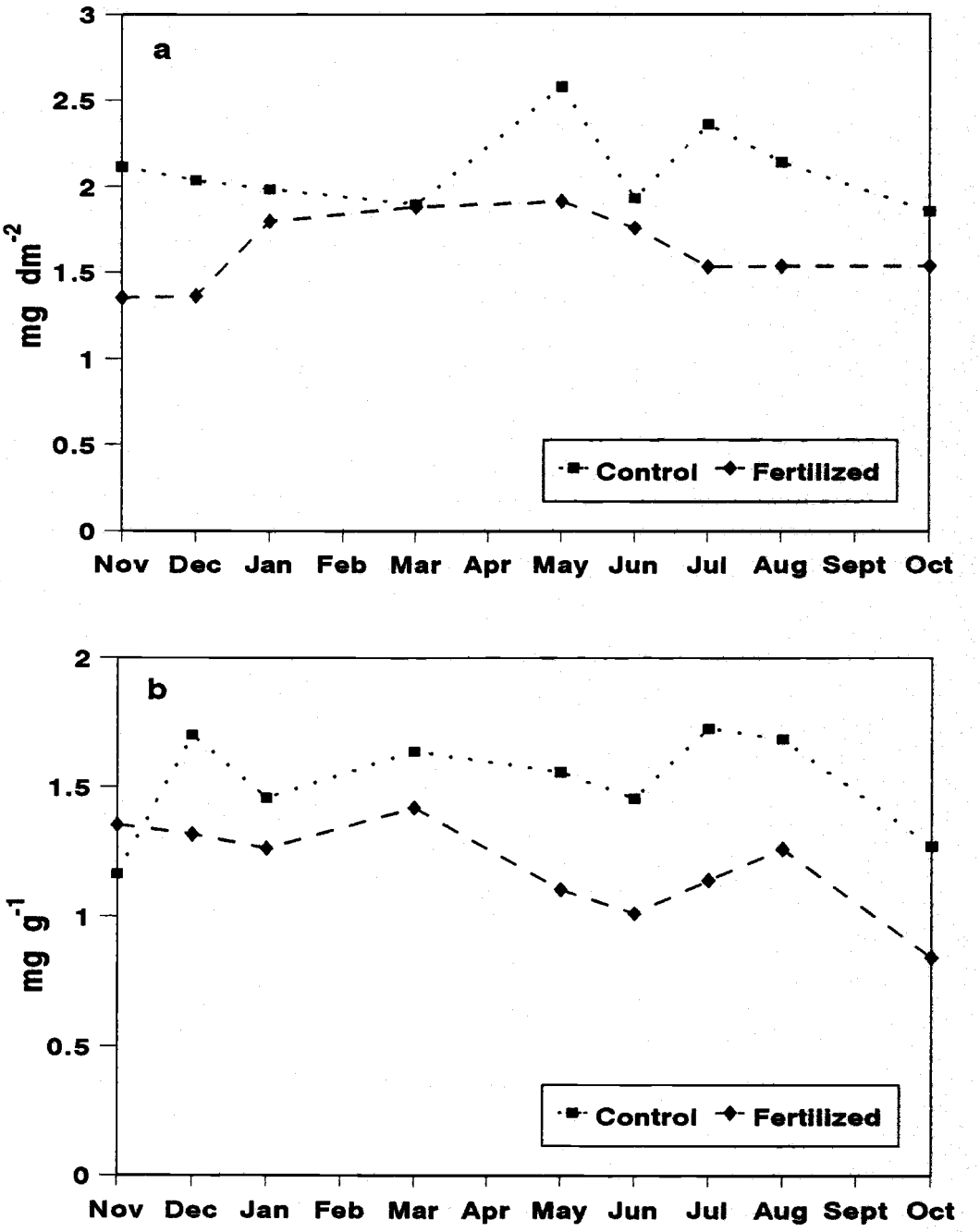

Fig. A.4. Phosphorus concentration of foliage from fertilized and unfertilized western hemlock through a 1-year measurement cycle. a) by unit area, b) by unit weight. Differences in a were significant with fertilization treatment, but not with sampling date or interaction effects.

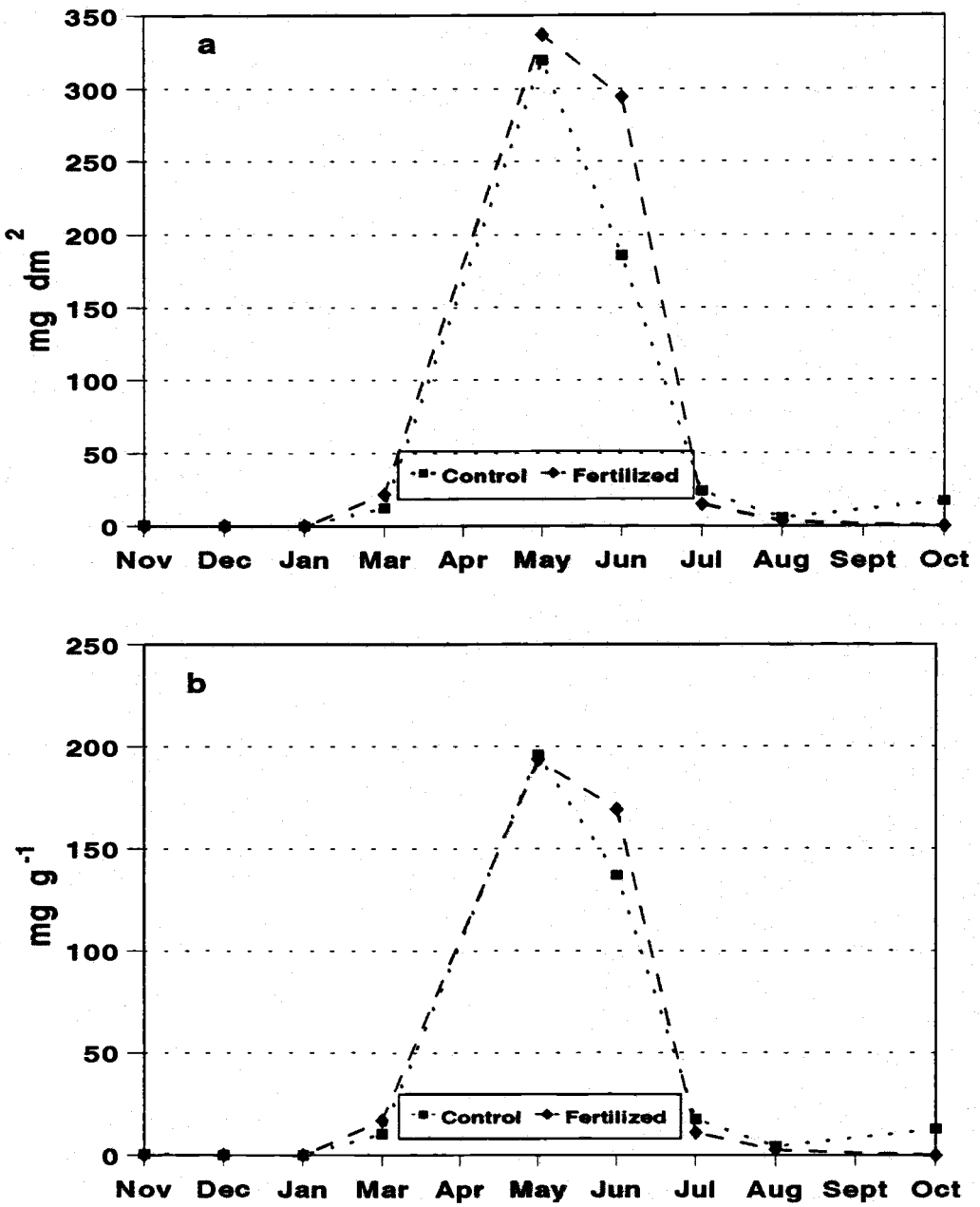

Fig. A.5. Starch concentration of foliage from fertilized and unfertilized western hemlock through a 1-year measurement cycle. a) by unit area, b) by unit weight. Differences in a were not significant with fertilization treatment. Differences with sampling date and interaction effects were significant.

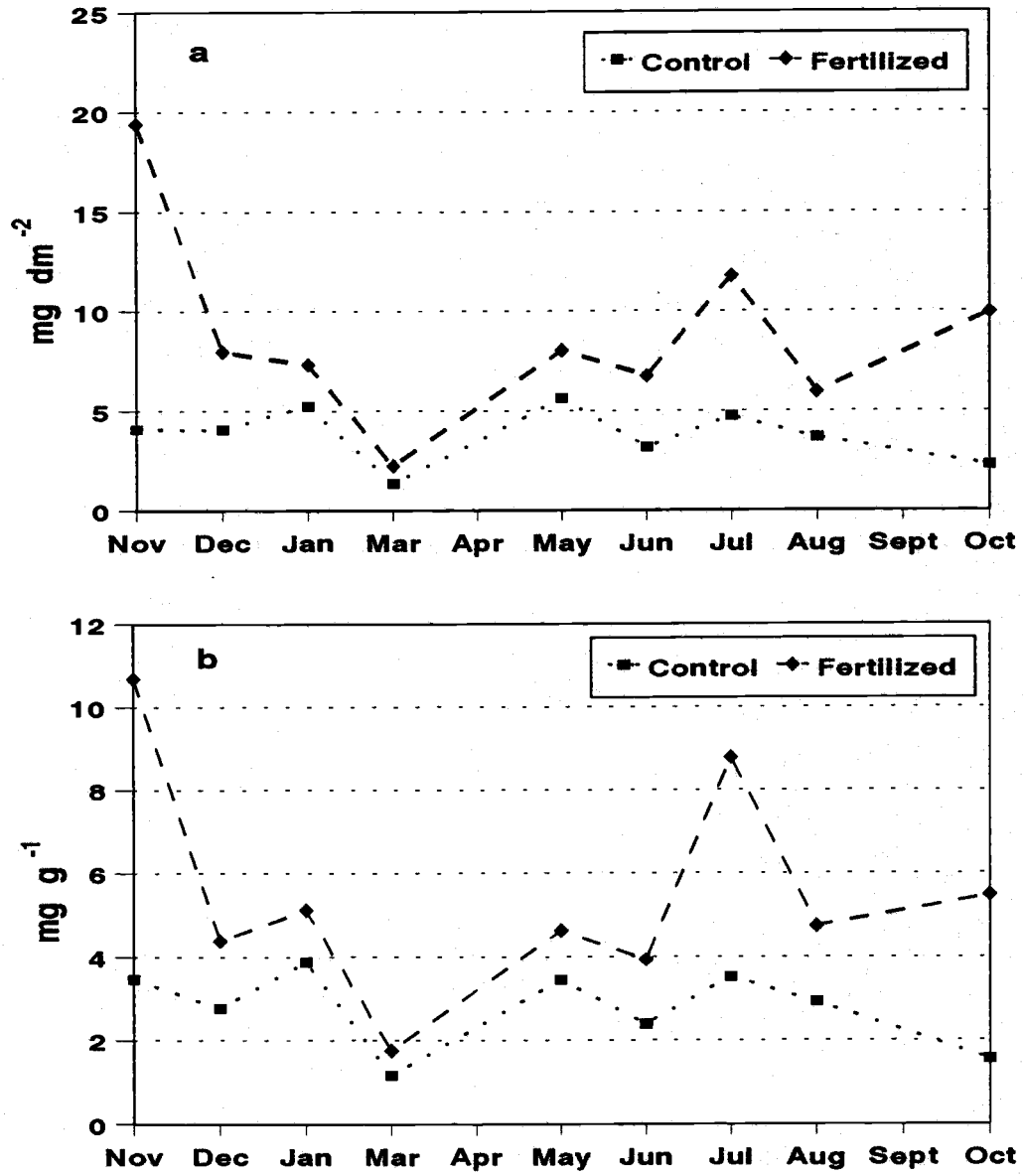

Fig. A.6. Amino acid concentration of foliage from fertilized and unfertilized western hemlock through a 1-year measurement cycle. a) by unit area, b) by unit weight. Differences in a were significant with both fertilization treatment and sampling date, but not with interaction effects.