Comparison of ecological and mensurational indexes of site quality and forest productivity in Pinus ponderosa stands of western Montana

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A COMPARISON OF ECOLOGICAL AND MENSURATIONAL INDEXES OF
SITE QUALITY AND FOREST PRODUCTIVITY IN Pinus ponderosa
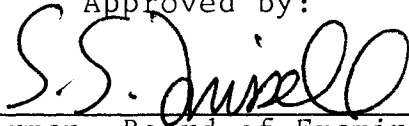STANDS OF WESTERN MONTANA

by Scott D. McLeod
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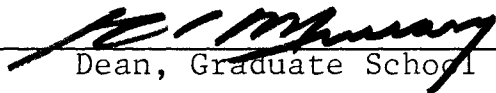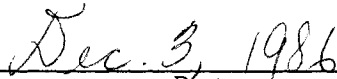the degree of

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   To evaluate the utility of alternative indexes of site
quality, site index (SI), leaf area index (LAI), an
available water index (AWI), and an estimate of gross
seasonal photosynthesis (gPSN) were compared to measured
productivity of ponderosa pine (Pinus ponderosa Laws.)
stands in western Montana. Coefficients of determination
for average annual volume growth and the selected site
quality indexes were, SI = 0.98; LAI = 0.93; AWI = 0.95;
and gPSN = 0.98. In addition, AWI and gPSN were very
useful for explaining differences in measured SI (R^2 =
0.95, and 0.96 respectively). Estimation of water supply
explained nearly as much of the variability in observed
ponderosa pine productivity as determination of site
index using stem analysis techniques, and is easily
calculated without depending on stand measurements. An
estimation of gross seasonal photosynthesis relates more
closely to productivity than simple quantification of
available water, and should be more accurate under a wide
variety of site temperature, water, and light conditions.

ACKNOWLEDGEMENTS

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INTRODUCTION

The determination of forest site quality is generally intended to quantify the potential for the production of forest products, usually stem wood (Carmean 1975). Various indexes of site quality have been devised because the term represents the abstract notion of "potential". Most commonly the forester relies upon an existing stand at the site in question and simply measures the productivity variable of interest, the assumption being that observed productivity closely approximates potential (Haaglund 1981). Unfortunately, mensurational approaches won't work without the proper stand conditions. Many of the stands in western Montana are the results of harvesting of the best trees originally existing. Other stands may exhibit poor stocking, dominance by sub-optimal species, or excessive levels of insect and disease problems. As a consequence what is present is often not at all representative of site potential. Even when mensurational estimates of site quality are accurate they provide no information on the controls of forest productivity nor of the relation between observed and potential productivity. This study explores the estimation of site quality from a causal factor or operational environment theory (Spomer 1973) perspective wherein biophysical factors and the processes which actually

determine productivity are quantified. By quantifying certain aspects of the environment controlling growth a more thorough understanding of the complexities of forest site quality can be gained.

Site index, a mensurational approach, is presently the most widely used indicator of site quality in western forests (Tesch 1981). It is defined as the height of dominant trees in an even aged stand at a specified base age. The determination of site index is usually accomplished by measuring the height and age of a number of dominant trees in a forest stand, accessing a set of guide curves with these data pairs, and inferring site index by interpolating height to the base age. Real site index can only be derived using stem analysis techniques or by measuring stands at the appropriate base age (Jones 1969).

A fundamental assumption of site index is that the height of dominant trees in a forest stand is relatively independent of stand characteristics such as density. However many research results indicate that as density increases site index decreases (Alexander 1967, Reukema 1979). Conversely the same studies often point out that total cubic volume increases with increasing density (Stiell 1967). Clearly, if wood (volume) production is

the true measure (or, desired product) of potential productivity then an index of site quality should not yield decreasing estimates when production is increasing! Finally, even under ideal stand conditions no information on the factors that control forest productivity is derived from a knowledge of site index.

What are the alternatives? Which operational factors can be quantified that will improve our understanding of and ability to calculate forest site quality? The availability of water is often referred to as having a predominant effect on the productivity of forest land. (Zahner and Donnelly 1967, Kozlowski 1982, Spittlehouse 1985). Early work relating water to forest growth concentrated on quantifying the effects of precipitation or soil water content on current annual increment (Dils and Day 1952, Zahner 1955, Fritts 1958). Increasingly, the impetus has been on defining long term trends in tree growth water relations (Satterlund 1981, Emmingham 1982). For example, summer water deficits can effectively curtail photosynthesis thus directly limiting potential production (Waring and Franklin 1979, Spittlehouse 1985). If pronounced seasonal drought is characteristic of a site, then quantification of available water should help assess potential productivity.

Mechanistic quantification of water availability is usually accomplished through calculations of seasonal or annual water balances (Grier and Running 1977, Black 1979). The necessary data for the calculation of a site water balance (SWB) includes estimations or measurements of precipitation, soil water storage capacity, and evaporative demand (Gholz 1982). The logic of such approaches is that the gross amount of water is trivial in comparison with the timing of availability (Zahner and Stage 1966), or without an indication of evaporative demand (Satterlund 1981). Evidence indicates that a SWB is strongly correlated with productivity (Grier and Running 1977, Gholz 1982, Giles et al 1985).

Due in large part to the expense of determining evaporative demand and in measuring soil water capacities at numerous sites, few practical applications of the SWB approach have been attempted. But, the operational implications are not lost as a significant relationship has been demonstrated between site water balance and leaf area index (LAI) (Grier and Running 1977, Gholz 1982). The underlying theory is that the amount of foliage a site can maintain is a direct manifestation of the sites water balance.

Several authors have reported high correlations

between LAI and measured forest productivity (Kittredge 1944, Tadaki 1966, Schroeder et al 1982). Additionally, current state-of-knowledge holds that LAI rises rapidly to a maximum, declines slightly and then maintains a relative equilibrium over several years (Waring et al 1978). The contention also exists that LAI is independent of stand density yielding consistent results within a given site quality (Knight et al 1981). Further, the ability to estimate LAI via remote sensing techniques is being developed (Running et al 1986). Thus, the large scale estimation of leaf area index/site water balances and the corresponding estimations of site quality may be possible.

Nonetheless LAI has problems similar to site index when used to indicate site quality, primarily it is still dependent on measurement of stand structural features. A desirable characteristic of the ideal site quality index is the capability to estimate potential irrespective of measurement of a forest stand at the site.

An accurate estimation of site quality that is completely independent of an existing stand may only be possible using modeling techniques (Reed 1980, Jarvis et al 1985). Currently there exists a far greater understanding of potential productivity at the physiological level (Troeng and Linder 1982), than at the

forest level (Lee and Sypolt 1974, Agren 1981). For instance, cold temperatures effectively limit photosynthesis through depression of leaf conductances and transpiration (Graham and Running 1984). Additionally, cellular water deficits and excessive evaporative demand can hinder or possibly completely halt gas exchange, by causing stomatal closure (Jarvis and McNaughton 1986). The same factors are occurring at the forest level but the effect on stem growth has never been quantified.

Knowledge derived from potentials at the process level should have general applications to plant growth. Attempts to extrapolate physiological processes from the cellular to the forest level have led to the creation of complex mechanistic models of plant growth (Lohammar et al 1980). One of these models, created to trace the development of climatic effects on tree growth, is DAYTRANS-C (a refinement of the previously documented H2OTRANS and DAYTRANS/PSN models, Running 1984a). By providing an estimate of the potential photosynthesis at a site, DAYTRANS-C might be a useful tool with which to estimate site quality without depending on measurement of a forest stand at the location of interest.

We believe that (1) quantification of the biophysical controls on productivity, such as water availability, can

provide an index to site quality independent of stand measurements, and (2) integrating the effects of water and temperature stress on potential photosynthesis via computer modeling gives us more accurate information on site quality enabling better predictions of current and future growth and yield. Further, for between site comparisons, the stands most representative of site quality are even aged, dominated by a single species, past the culmination of periodic annual increment, and at more or less the same age. The site quality indexes selected for comparison are site index (SI), leaf area index (LAI), available water index (AWI), and an estimation of photosynthesis (gPSN). The productivity standard selected is average annual stemwood volume growth of the stand.

METHODS

Study Sites

Study site selection was designed to represent the apparent range of productivity for ponderosa pine stands in western Montana, and to minimize extraneous sources of variation in productivity which could adversely affect our focus on site quality relationships. Primary sources of variation in productivity which could mask true site quality effects include the species present, extremes in stand density, very old or young stands, and stand establishment conditions and history, particularly management practices (Haaglund 1981).

Different species grow at different rates under the same conditions, optimum growth conditions probably differ by species also (Waring and Schlesinger 1985). The noise introduced to mensurationally derived site quality estimations by species differences was therefore eliminated in this study. All sample stands were naturally regenerated, even aged ponderosa pine (Pinus ponderosa Laws.) stands with no evidence of management intrusion, a minimum of mortality, freedom from insect or disease problems beyond endemic levels, and of sufficient age to ensure the culmination of periodic annual volume increment had occurred. Our intention was to sample stands that had already achieved the maximum growth attainable at the site in question under full stocking

conditions, and were all at approximately the same stage
in development (i.e. same point on the growth curve). Our
sample stands were in effect the finest unmanaged even
aged ponderosa pine stands to be found.

As explained earlier stand density can have a
pronounced effect on observed productivity (Lynch 1958,
Alexander 1967). Control of this source of variation was
accomplished by replication of sample plots in discrete
density classes (Stand density indexes = 260-290, 320-350,
and 380-410, [Reineke 1933]; which roughly correspond to
crown competition factors = 100, 150, and 200, [Krajicek
et al 1964]). This approach to density allowed us to
focus on the relationships between selected site quality
indexes and productivity, unencumbered by density effects.
As a result differences in productivity between stands may
be logically attributed to differences in site quality
(Curtis and Reukema 1970).

Stand Measurements

Sample sites consisted of six 1/25 hectare (1/10
acre) fixed plots, two in each pre-selected density class.
All trees on a plot standing and down were measured for
dbh, height, and species. Two increment cores were taken
from each live tree for the determination of age and
sapwood area. Total height and dbh were used to calculate
tree volumes using the equation for ponderosa pine trees

reported by Faurot (1977). Tree volume divided by breast height age was summed for all trees on a plot to determine average annual growth. This gave us a stand level total stem growth per hectare which is of significance to potential in a relative sense, but is not meant to imply a current growth rate, nor to predict future growth of the stand, only an average of what the stand has realized in the past.

Site Quality Estimators

A comparison of site quality indexes necessitates selection of a standard to be compared with. What is the dependent productivity variable that a site quality index is attempting to estimate? For lack of an alternative site index is often chosen (Spurr 1955, Hunter and Gibson 1984). Despite our unhappiness with site index (primarily a consequence of depending on existence of a perfect stand which can be measured to produce an estimate of site quality), we felt it would be a useful exploration of productivity relationships to treat site index as a dependent variable in one set of comparisons. We also treated site index as an independent variable in the prediction of a measure of productivity that more closely approximates the variable of interest, average annual cubic volume growth per hectare per year (1 m^3/hec = 14.3 ft^3/acre). The other site quality indexes were treated as

independent variables in the prediction of site index and average annual growth.

Site Index

Site index was determined using stem analysis techniques obviating the need for, and imprecision of the guide curve method. The 2 tallest trees per plot were sectioned in the field; subsequently the sections were measured on a Technology Dynamics Inc. Digital Measuring System Model 1000 ring reading machine and total height at 50 years breast height age determined. To arrive at an actual site index we averaged the heights of the 12 stem analysis trees for each stand. We circumvented many of the problems faced when inferring site index, by calculating real site index, using it at its best and most indicative of site quality (Spurr 1956, Daubenmire 1961, Carmean 1975).

Available Water Index

Available water index (AWI) was calculated as the sum of annual precipitation, and soil available water capacity (AWC). Precipitation was taken from long term averages reported in the annual climatic summaries published by the National Weather Service, NOAA. Although this index is not ecologically elegant its simplicity and easy calculation make it operationally useful for site quality estimation in water limited sites.

Available water capacity (AWC) was calculated as a function of soil depth, coarse fragment content, bulk density, and an estimation of plant available water (PAW), or the difference between -0.03 MPa (field capacity), and -1.5 MPa water (lower limit of available water, or permanent wilting point), (Fralish, et al, 1978). Six soil pits were excavated in each stand and the soil profile described according to standard procedures (SCS, 1975). The soil descriptions gave us assurance against sampling stands growing on more than one soil type, thereby introducing further variation in productivity. From the pits, intact soil cores were removed for the laboratory determination of PAW (using a pressure plate apparatus), and bulk density. The calculation of AWC resulted in a percent water by volume or depth of soil. Therefore a simple multiplication of soil depth by AWC gives a total plant available water capacity for the root zone.

When dealing with below ground processes, as we are when contemplating tree growth water relations, some assumptions relating to rooting characteristics must be made. We assumed, (1) equal rooting depth for each stand (Cox et al 1960), (2) equal water extraction capabilities for trees in different stands (Hillel 1984), and (3) PAW represents what is actually available to the tree roots

(Brown 1981).

The AWI is similar to an annual SWB except that
evaporation is ignored. Although usually considered
necessary, two characteristics of our study sites justify
this treatment of evaporation, (1) the same meso-scale
climatic conditions prevail at each site (Running et al
1986), and (2) physiographic conditions such as slope,
aspect, and elevation are also roughly equivalent (Table
1).

Leaf Area Index

Recognizing that many leaf area studies have been
based on diameter derived estimates of LAI (Kittredge
1944, Waring et al 1978), and the preponderance of
evidence indicating the inadequacies of such estimations
(Snell and Brown 1978, Marshall and Waring 1986) we
decided to use sapwood area to calculate leaf area. LAI
is believed to be limited by the ability to supply water
to the crown, meaning that all the components interacting
to control water availability from precipitation to
evaporative demand play a role in determining the LAI that
can be maintained at a site (Kaufman and Troendle 1981).
Factors other than water availability affect dbh, such as
stand density and tree age. Therefore diameter based
equations may inaccurately predict individual tree leaf
area, and stand LAI. In fact, LAI estimated from dbh

results in nothing more than an expansion of plot basal area.

Leaf area index was determined using a simple linear regression model developed via destructive sampling of trees in the same study stands:

$$LA = -11.55 + 0.264 \ SWBH$$

where: LA = total tree leaf area, m^2

   $SWBH$ = sapwood area at breast height, cm^2

   $n = 40; \ R^2 = 0.93.$

Leaf area was computed for each tree using the sapwood areas determined from increment cores. Summation of individual tree leaf areas divided by plot size results in total tree leaf area on an areal basis (i.e. leaf area index, LAI).

Photosynthesis Estimations

DAYTRANS-C is a stand level daily resolution model of tree water balance coupled with the photosynthesis equations in FAST-P (Lohammar 1980; Running 1984a, 1984b). DAYTRANS-C first calculates a hydrologic mass balance for a stand, including precipitation and snowpack inputs, surface runoff, evaporation, transpiration and groundwater seepage outputs. From this soil water balance, a measure of leaf water potential is derived. Assumed leaf water potential for stomatal closure is -1.65 MPa. The average leaf conductance of the canopy is calculated with controls

by leaf water potential, incoming shortwave radiation
attenuated through the canopy, humidity, and temperature,
including a special frost reduction (Graham and Running
1984). Maximum leaf conductances for water vapor and CO_2
are fixed at 0.0016 and 0.0008 m/sec respectively.
Transpiration is calculated using the Penman-Monteith
equation with a fixed aerodynamic resistance of 5 s/m; and
a net radiation component divided by projected leaf area
index to reflect how radiation is absorbed by a
multilayered canopy (Running 1984a).

The photosynthesis routine multiplies a CO_2 diffusion
gradient by the radiation and temperature controlled
mesophyll and stomatal conductances generated by the
model. The assumed light compensation point is 432
$KJ/m^2/day$. Minimum and maximum temperatures for
photosynthesis are 0° C, and 37° C, which sets a maximum
effective temperature of 19° C. Net daily photosynthesis
is arrived at by subtracting a temperature-controlled
night respiration component from the predicted daylight
gross photosynthesis (Running and Nemani 1985). Net daily
photosynthesis calculations are summed over a growing
season giving an indication of gross seasonal
photosynthesis.

Interpretation of the DAYTRANS-C output as a site
quality index required simulation of seasonal

photosynthesis using site specific input and driving variables of microclimate, and soil water capacity (field capacity). A hypothetical stand of fixed dimensions was programmed into the model to allow simulation of gross photosynthesis on an areal basis. Leaf area index was fixed at 6, and biomass of carbon in stems and roots fixed at 1.0 e^5 and 5.0 e^4 kg/ha respectively. Consequently output could be viewed as representing the effect of site variables on potential growth totally independent of the stand currently growing at the site.

Site microclimates were simulated using the MT-CLIM model introduced by Running et al (1986). MT-CLIM is a daily resolution model that allows extrapolation of climatic data collected in one locale to another with corrections for slope, aspect, and elevation. Best results are obtained when extrapolating over horizontal distances of less than 100 km. Base stations monitoring simple climatic variables were less than 20 km from each of our study sites. In addition elevation, slope, and aspect differences were minimal between base stations and study sites (Table 1). Extrapolations were made of data collected at four USFS ranger stations (National Fire Danger Rating System) and one National Weather Service station. MT-CLIM simulations required as input variables maximum and minimum temperatures, and precipitation

measured daily at a base station. The MT-CLIM model
produces daily daylight average temperature, night minimum
and dewpoint temperatures, relative humidity,
precipitation, and daily shortwave radiation for the site
of interest. These outputs correspond to the driving
microclimatic variables necessary for the DAYTRANS-C
simulations used to predict site quality.

At initiation of DAYTRANS-C model runs on year day
(YD) 91 soils were assumed to be at field capacity with a
snowpack water content equal to the previous 30 days
average precipitation. Simulations were terminated on YD
294. Output variables of interest included transpiration,
evaporation, outflow, leaf water potential, soil water
content, and photosynthesis.

This is the first application of the DAYTRANS-C model
to predict site quality. Previous applications have
indicated the models responsiveness to microclimatic
effects (Running 1984b), and its utility in predicting
tree water stress (Donner and Running 1986).

RESULTS AND DISCUSSION

Our first comparisons involved estimating the
correlation between site index and the ecologically
derived site quality indexes (Table 2). In the pure
even-aged ponderosa pine stands sampled both an AWI and
gPSN were highly correlated with SI (coefficient of
determination = 0.95, and 0.96 respectively, Figures 1 and
2). Although site index by itself contributes scant
knowledge to our understanding of what controls tree
growth we have explained 95% of the variation in this
accepted index of productivity with a simple one factor
analysis (AWI), reaffirming the importance of water to
forest productivity in the ponderosa pine stands sampled.
Conversely, we've taken a complex mechanistic prediction
of photosynthesis which integrates the effects of climate,
and physiographic position and also explained most of the
variation in site index. Obviously SI is related to site
quality, but just as important is that quantification of
causal environmental factors explains most of the
variation in SI, without depending on stand measurements.
If we can explain and quantify the controls on
productivity we can predict with some accuracy and
confidence, potentials of sites not measured.

As early as 1918 Bates claimed height growth (and so
site index) was completely dependent on water
availability. Since then other researchers have reached

similar though usually less extreme conclusions (Basset 1964, Kozlowski 1982). Knowing that much of the variation in site index can be explained from a causal viewpoint we focused our attention on predicting a more satisfactory measure of productivity, average annual cubic volume increment. Again the explanatory power of the AWI and gPSN estimates is high (R^2 = .95, and .97 respectively, Figures 3, and 4). LAI also explained a significant amount of the variation in productivity (R^2 = .93, Figure 5). Site index worked as well as any of the other indicators (R^2 = .98).

Although SI (or height at age 50) accounted for a substantial proportion of the variation in mean annual volume growth it should be remembered that tree height is one of the three components determining tree volume (height, diameter, and form). Therefore in stands that meet all the criteria implied for accurate estimation of SI, its measurement should naturally exhibit the strong relationship with volume growth demonstrated in this study. Unfortunately, within a stand SI varied by as much as 5.5m (18 ft), with the highest density usually associated with lower SI (Martin, manuscript in prep.). Concurrently, average growth was highest on the densest plots. The sites with the lowest AWI exhibited the greatest reductions in SI, due to stand density. At the

wet extreme, SI was less affected by density, but the influence was much greater on measured growth . Even when applied in stands carefully selected to be perfect and free from extraneous influences on productivity, the relationship between SI and growth appears to be inconsistent depending on stand characteristics as well as site quality.

LAI's for our stands fell within ranges published for pine forests from other areas (Tadaki 1966, Gholz 1982). LAI predictions showed clearly the positive relation with stand growth. Kittredge (1944) using American and European data , Tadaki (1966) in Japan, and Schroeder et al (1982) in eastern Washington have demonstrated similar trends. Comparison of LAI and growth indicated the positive relation with respect to density, measured LAI increased with density as did growth, in contrast to earlier assumptions of the independence of LAI from density effects. As a consequence single point estimations of LAI may correlate better with productivity than SI. Unfortunately, the relationship may only be consistent when used within species. This problem is also common to SI estimations and further demonstrates the difficulties faced when evaluating potential productivity from stand measurements.

The calculations of AWI indicated the contribution of

precipitation was considerably larger than that of soil AWC. Much of the annual precipitation falls as snow during the dormant season and snowmelt water is an important source of moisture early in the season. Water stressed conditions may be put off for one to many weeks as a result of utilization of snowmelt water. Also, because water absorption below the assumed rooting depth may be significant an estimate of annual precipitation although gross, represents the total entering the system (our stands were basically flat, hence we assumed little or no subsurface water flow is adding to the system).

Several works have reported on the strong relationship between SWB and productivity (Satterlund 1981, Spittlehouse 1985, Gholz 1982). The AWI used in this study is also highly correlated to measured productivity. We feel this is an important fact because it allows the gross estimation of productivity using readily accessible variables which are independent of a stand at the site in question. As a result, in areas with similar water limitations, the rapid, large scale estimation of potential productivity patterns may be possible without field measurements, clearly a desirable capability.

Results from the DAYTRANS-C simulations agreed very closely with productivity measurements. Predicted gPSN

values, are within the realm of published photosynthesis rates for coniferous forests (Mohren et al 1984), but do not attempt to account for differences in allocation patterns believed to vary according to site quality (Linder and Rook 1984), nor for respiration losses, and so should not be viewed directly as growth. Simulation results provide a tool with which to examine the seasonal course of potential productivity, allowing greater interpretive power involving the mechanisms determining growth than can be garnered with simpler indexes.

Simulations indicate that the sites with low AWI, were experiencing some moisture stress as early as June 8. By July 20, at Edith, the site with the lowest AWI (46.6 cm), pre-dawn leaf water potentials were in excess of -1.5 MPa. At this extremely water limited site less than 2% of the total predicted seasonal photosynthesis (10.6 metric ton C/hectare/year), occurred after August 15. The Sloway and Plains sites also had low AWI, and experienced similar water stress patterns and curtailment of photosynthesis.

The Sorrel site had identical microclimatic conditions as Edith but a higher soil water capacity (23.5 cm. vs. 18.8 cm) and so avoided water stress for about 15 days. Additionally, late season photosynthesis accounted for 10% of the total at Sorrel. The predicted gPSN for these two sites differed by about 20%, almost identical to

the difference in AWI. Troy, which has a higher AWI, experienced no water stress until July 8 and photosynthesis after August 15 amounted to 15% of the seasonal total. Noxon, the wettest site, with the highest AWI and soil water capacity (29.5 cm), was virtually unstressed the entire growing season. Predicted pre-dawn leaf water potentials were never more than -0.7 MPa, and photosynthesis after mid August amounted to almost 30% of the seasonal total. Predicted water potentials were in accordance with measured potentials from published results (Graham and Running 1984, Donner and Running 1986).

Seasonal evaporation estimated in the simulations was quite similar between sites (mean = 21.5 cm, std. dev. = 1.5 cm), except for Noxon where greater precipitation in combination with low soil water potentials allow more evaporation to occur. These evaporation results support our use of an AWI. Predicted transpiration was coincident with the trend exhibited by photosynthesis, a result of the effect of water deficits on photosynthesis.

The pattern of photosynthesis predicted for the various sites is dependent on temperature as well as water availability. The sites with the highest (Noxon), and lowest (Sloway) predicted gPSN, exhibit greatly different patterns of photosynthesis (Figure 6), and transpiration (Figure 7). At Sloway higher early season temperatures

allowed more rapid photosynthesis until about July 10 when soil water was nearly depleted, and low leaf water potentials virtually halted transpiration. On the contrary, Noxon with its lower spring temperatures, started slower, but continued photosynthesis at near potential rates throughout the growing season because of greater water supply. The predicted gPSN for these two sites differed by more than two fold, as did the measured annual growth. The much longer water defined growing season at Noxon could easily account for the greater productivity observed there.

Judging by the pre-dawn water potentials predicted by DAYTRANS-C, summer drought effectively halts photosynthesis at many sites in Montana by mid August, even though temperatures remain near optimum levels for several more weeks. Amelioration of high water stress can be accomplished by precipitation of sufficient magnitude that soil water content is recharged (peaks in the soil water depletion line, Figure 7). The effect on transpiration though is unnoticeable and any relief is likely to be temporary. Furthermore the contribution to soil water by precipitation events of less than 1.3 cm is negligible, due to canopy and litter interception and evaporation.

While recognizing the dangers of extrapolation, some

inferences can be made. Based on evidence from simulations indicating minimal water stress development, Noxon probably represents the upper limit of increasing site quality from increased available water. Additional water would probably have little effect on photosynthesis without greater radiation loads, more nutrients, or a longer temperature defined growing season. The AWI at the Sloway site can be taken as indicative of a water limited site, an increase in available water would almost certainly result in greater growth. Simulations support the contention that water limits the productivity of ponderosa pine stands in Montana, predicting a virtual cessation of transpiration and photosynthesis in many sites after July 15.

CONCLUSIONS

The current reliance on mensurational methods to indicate site quality is inadequate, largely because without a stand to measure they are useless. Furthermore unless the stand meets all the assumptions implied for accurate estimation of site quality the results can be misleading. A third problem is the species specific nature of mensurational indexes, i.e. what does a SI 50 for ponderosa pine mean if we want to grow western larch at the site. The success of SI here is largely because stands were chosen to be perfect and SI was determined as accurately as possible through stem analysis. Leaf Area Index suffers from some of the same problems as SI, especially the dependence on stand measurements. Although both indexes showed high correlations with stand growth, they are still only manifestations of a sites potential, and so do not explain what is controlling growth.

The presentation of simple coefficients of determination is only meant to show that significant relationships exists. We base our conclusions as to the acceptability of the various site quality indexes on ecological principles, and general applicability. For example, we conclude that the gPSN index is preferable to all the other indexes, but not solely on the basis of R^2, rather we look at the range of conditions under which each can be utilized to produce accurate estimates. Site index

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is a complete failure when it can't be measured, likewise with LAI. The AWI is quite appropriate when applied to the water limited sites sampled, but cannot be expected to provide much information when factors other than water availability become limiting at a site, such as high elevation, north slopes where the interactions between radiation and temperature defined growing season ultimately exert the primary controls on potential productivity.

However, in low elevation forest stands of western Montana long periods with no precipitation occur during the growing season. Therefore water availability is important in determining productivity. Results from this study support the contention that water controls, to a large degree the patterns of productivity demonstrated by ponderosa pine stands of western Montana.

Water is the most important factor controlling site quality in this study, but is only one of the environmental factors determining growth. DAYTRANS-C integrates the effects of water supply and both the timing and absolute magnitude of other climatic factors to estimate the seasonal photosynthesis possible at a site. The gPSN index is also independent of measurements of the current stand. Our results demonstrate a high correlation

between the gPSN index and measured forest productivity ($R^2 = 0.98$).

In conclusion, estimation of water supply explains nearly as much of the variation in observed ponderosa pine productivity as determination of site index using stem analysis techniques; and is easily calculated without depending on stand measurements. An estimation of gross seasonal photosynthesis relates more closely to productivity than simple quantification of available water, and should be more accurate under a wide variety of site temperature, water, and light conditions.

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Table 1. Site physical and stand characteristics.

Location	Slope (%)	Aspect (deg)	Elevation (meters)	Stems #/ha	Basal Area (m2/ha)	Age (yr)
SLOWAY	<5	FLAT	825	1124	38.1	85
EDITH	15	190	975	971	40.2	90
PLAINS	<5	FLAT	700	897	42.5	77
SORREL	10	190	975	568	49.4	88
TROY	<5	FLAT	610	860	44.3	59
NOXON	<5	FLAT	640	452	50.0	66

TABLE 2. Site Quality and Productivity Indexes.

LOCATION	AWI (cm)	SI (m/50yr)	LAI (m^2/m^2)	gPSN (MT-C/yr)	Growth (m^3/ha/yr)
SLOWAY	49.7	16.8(1.79)a	5.20(0.54)	9.6	3.55(0.39)
EDITH	46.6	17.4(2.50)	5.37(0.71)	10.6	3.97(0.32)
PLAINS	53.6	20.6(1.67)	6.50(0.42)	11.1	5.30(0.37)
SORREL	53.0	22.2(0.28)	6.94(1.03)	13.0	5.87(0.83)
TROY	78.2	27.4(1.01)	7.30(0.76)	19.0	8.29(0.73)
NOXON	95.2	30.0(0.24)	8.40(0.93)	21.9	10.61(1.16)

aMEAN(std. dev.)

$$SI = 6.02 + 0.26 \ (AWI)$$

$$R^2 = 0.95$$
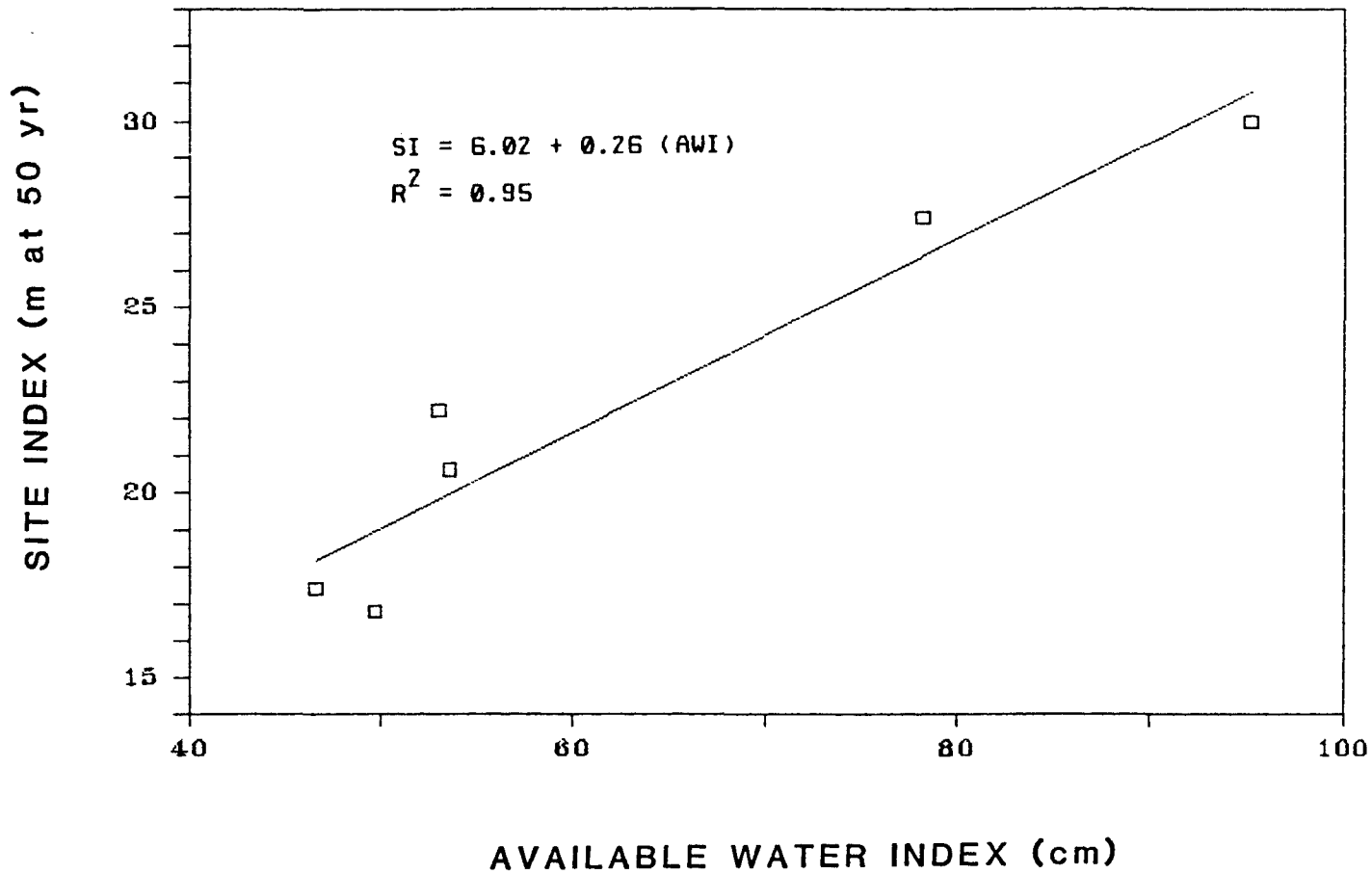
FIGURE 1. The relationship between site index (SI) and an available water index (AWI) in ponderosa pine stands of western Montana. AWI equals the sum of average annual precipitation and soil water capacity. SI is the average of 12 dominant trees per stand and is determined using stem analysis techniques.
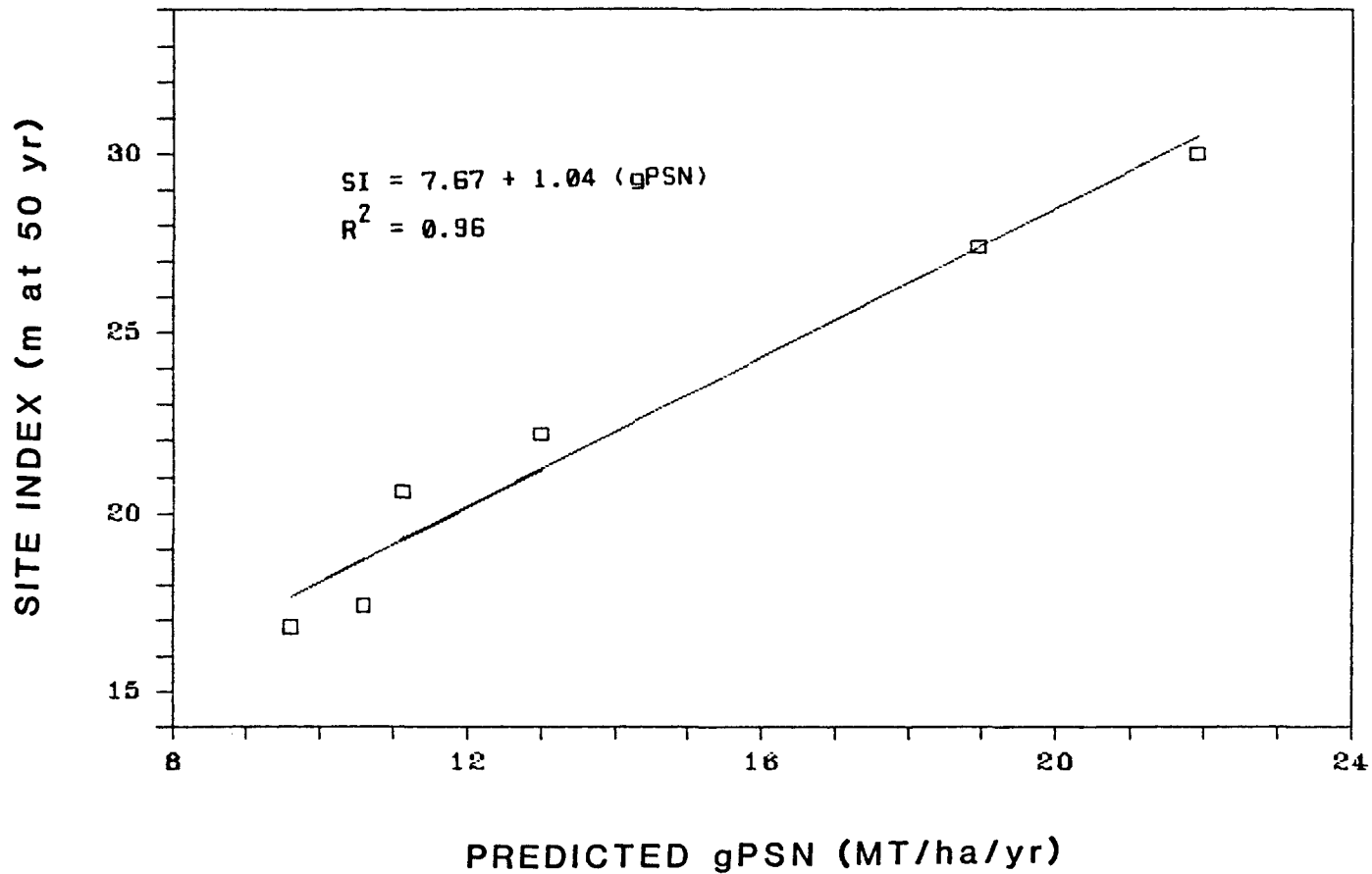
FIGURE 2. The relationship between site index (SI) and gross photosynthesis (gPSN) predicted by the DAYTRANS-C model. gPSN is in metric tonnes of carbon per hectare per year. SI is the average of 12 dominant trees per stand and is determined using stem analysis techniques.
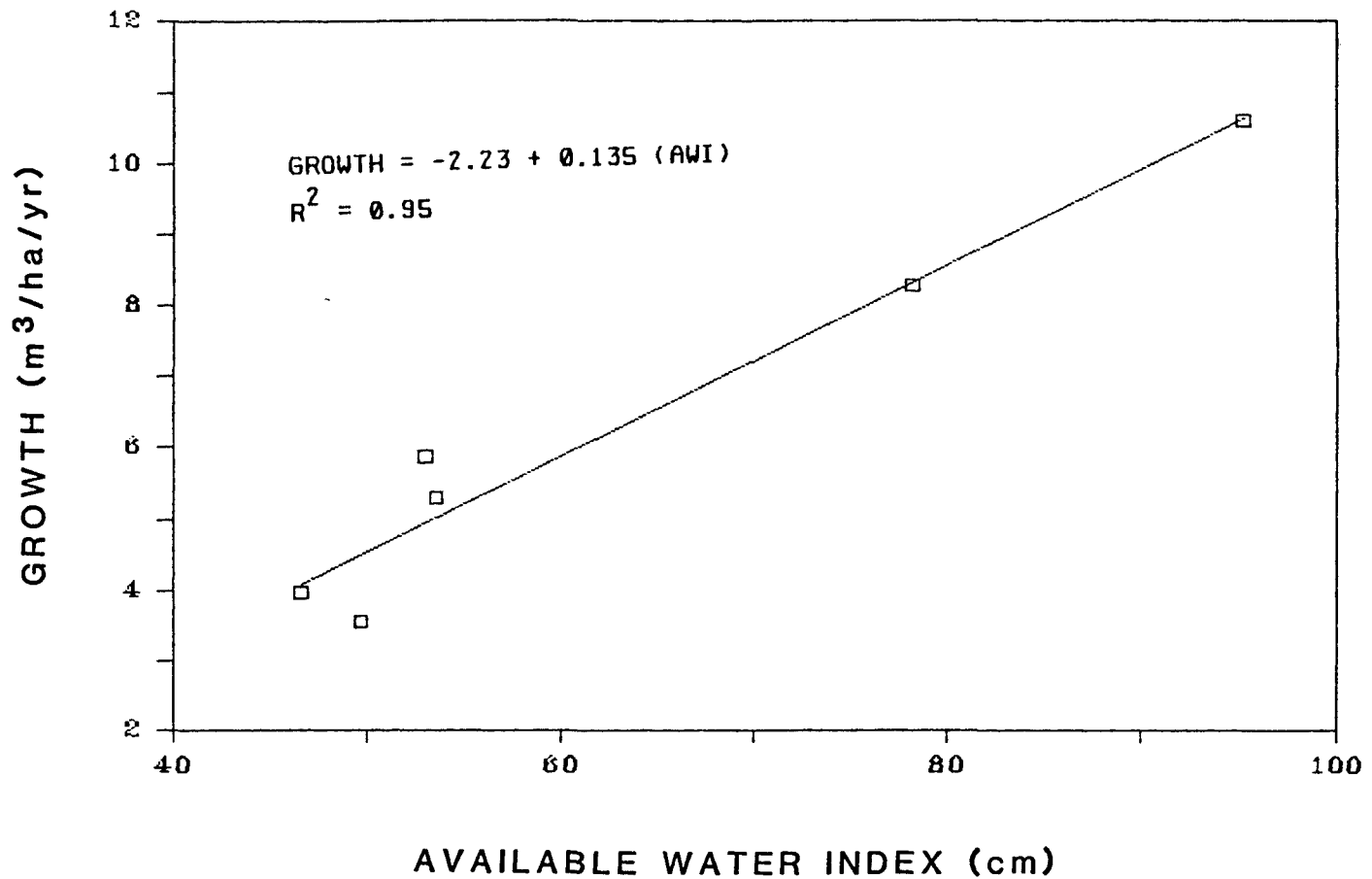
FIGURE 3. The relationship between average annual stemwood volume increment and an available water index (AWI) in even aged stands of ponderosa pine. AWI is the sum of average annual precipitation and soil water capacity. Growth is determined from averages of 6 1/25 hectare fixed plots, and is total stem growth per year.
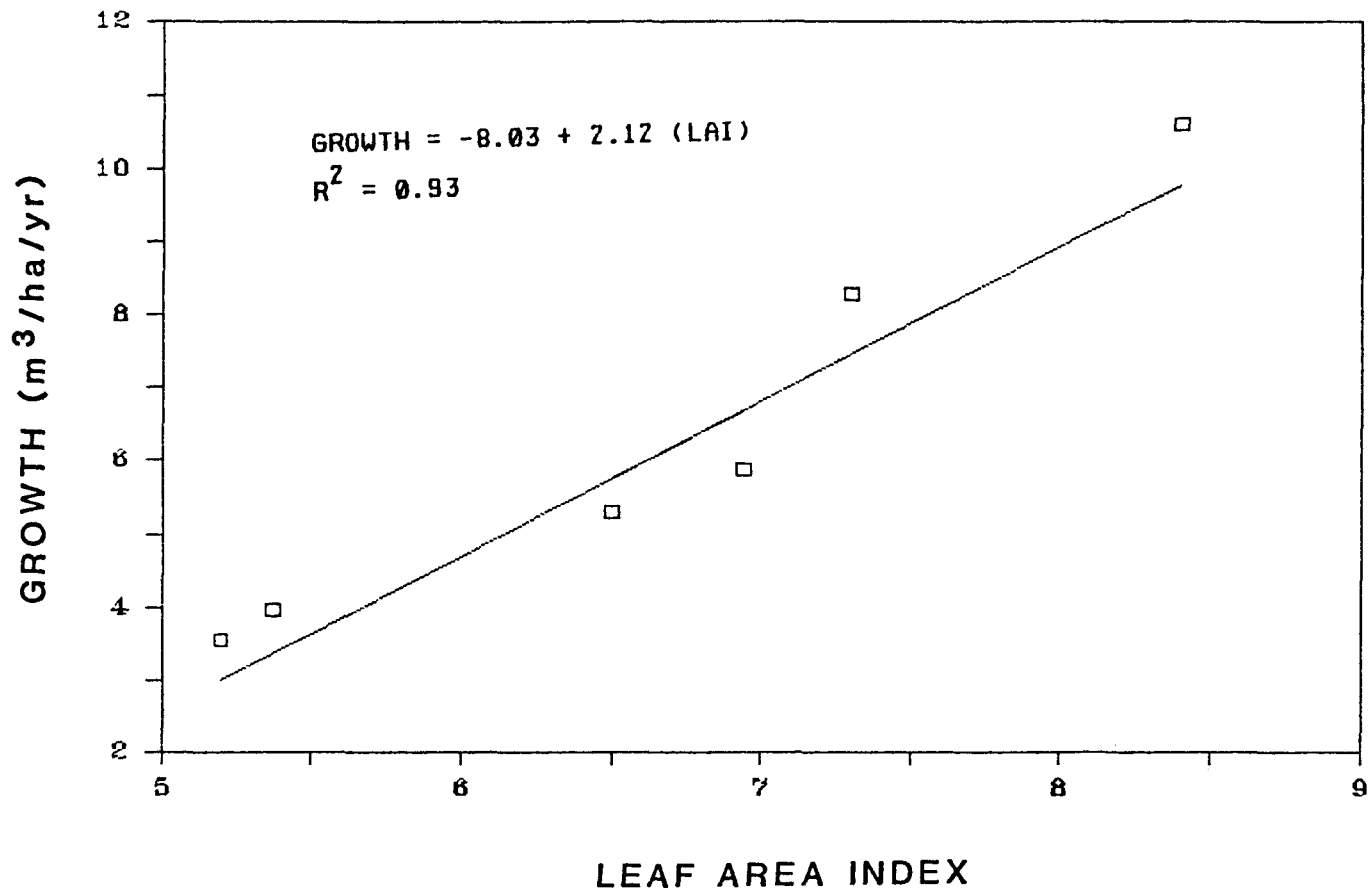
FIGURE 4. The relationship between average annual stemwood growth and leaf area index (LAI) in even aged stands of ponderosa pine in western Montana. LAI was computed from sapwood area and is total or all-sided LAI. Growth is the yearly average total stemwood volume increment determined from 6 1/25 hectare fixed plots.
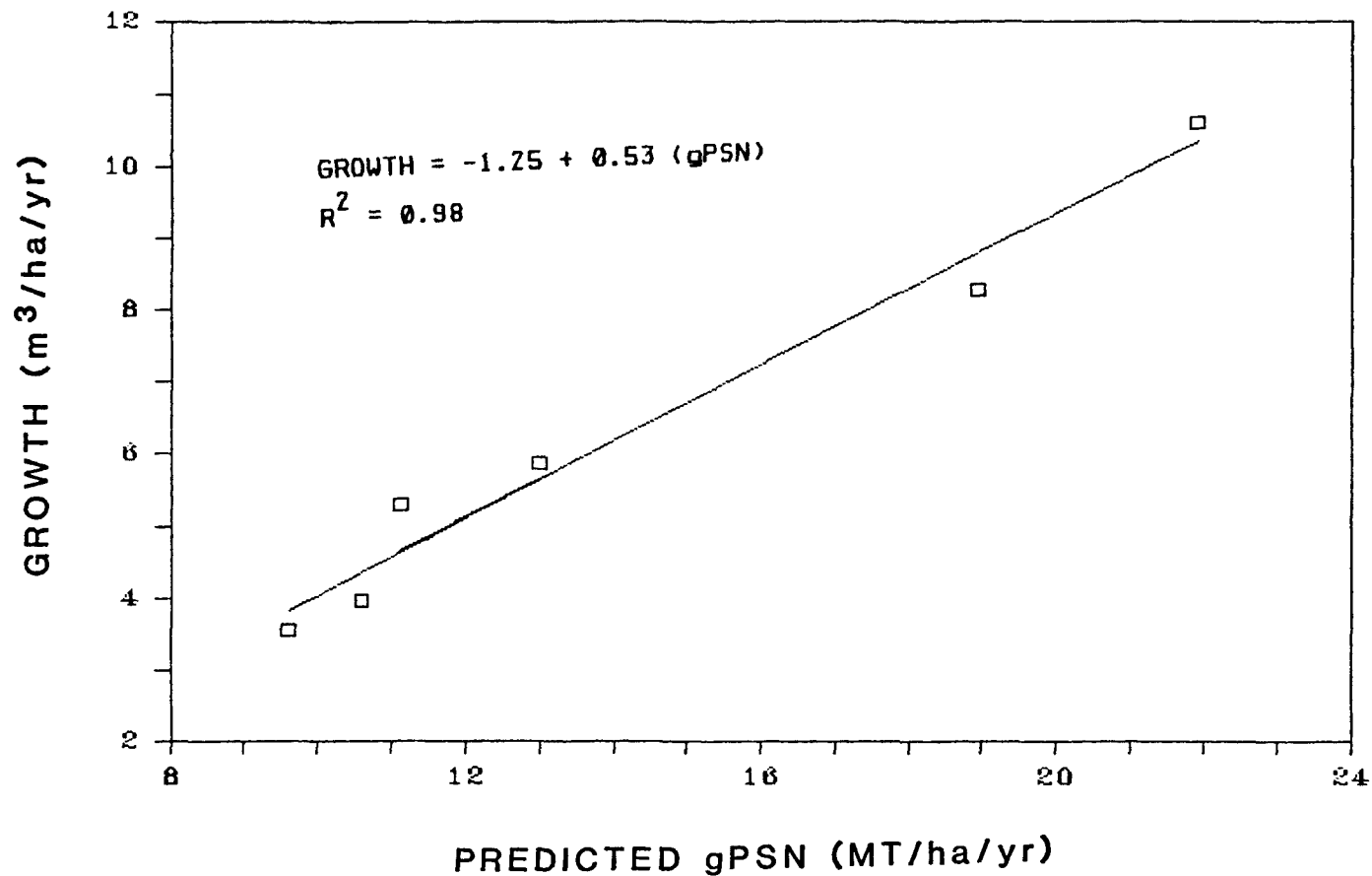
FIGURE 5. Average annual stemwood growth in relation to gross
photosynthesis predictions from the DAYTRANS-C model. Model runs represent
the potential of hypothetical stands given site specific driving variables
of climate and physiography. Growth represents the total stemwood yearly
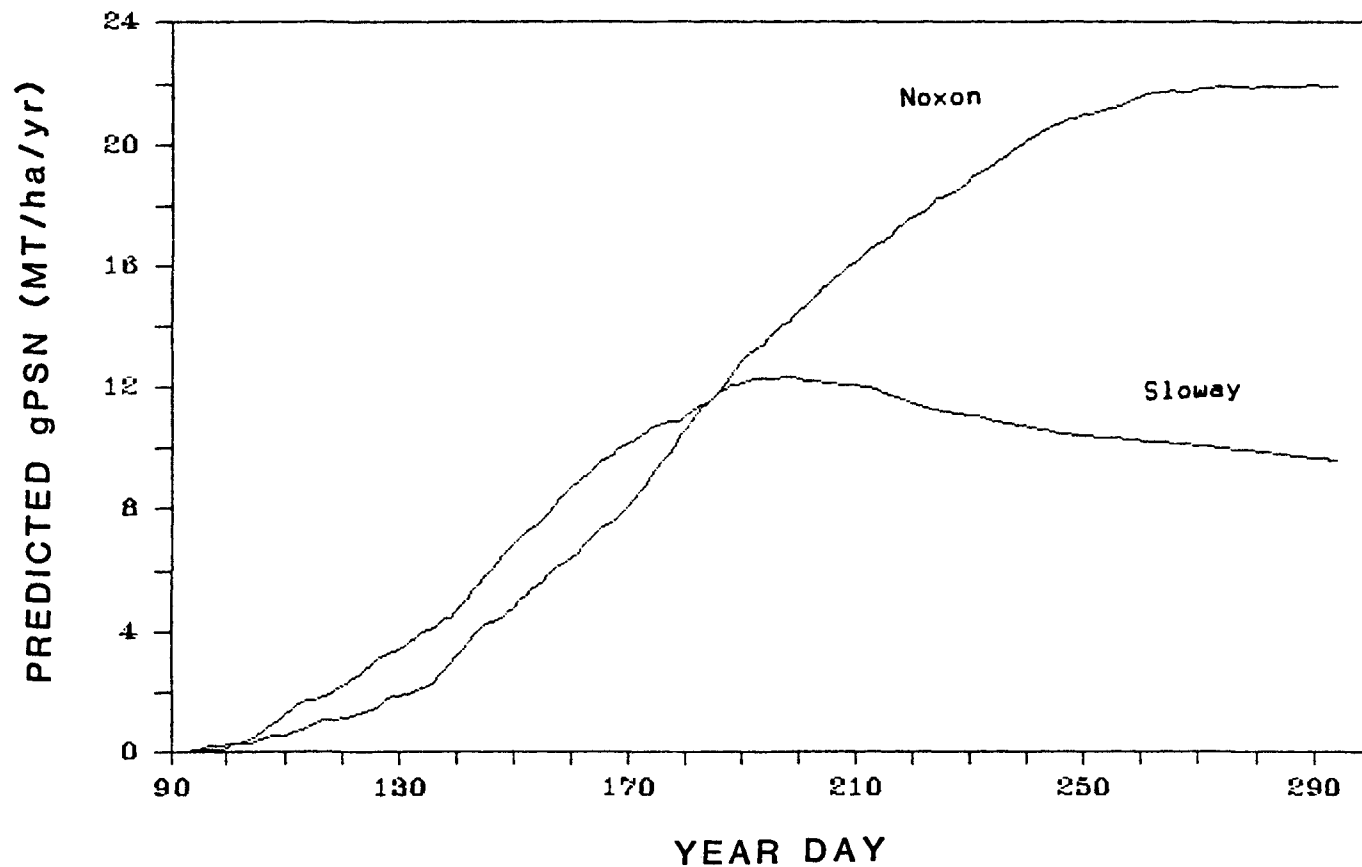average increment determined from measurements of 6 1/25 hectare fixed
plots.

FIGURE 6. Seasonal course of gross photosynthesis (gPSN) at sites with the highest (Noxon), and lowest (Sloway) predicted gPSN. The pattern of photosynthesis mimics that of transpiration indicating that the length of the growing season, and hence productivity for many ponderosa pine stands is determined by water availability.
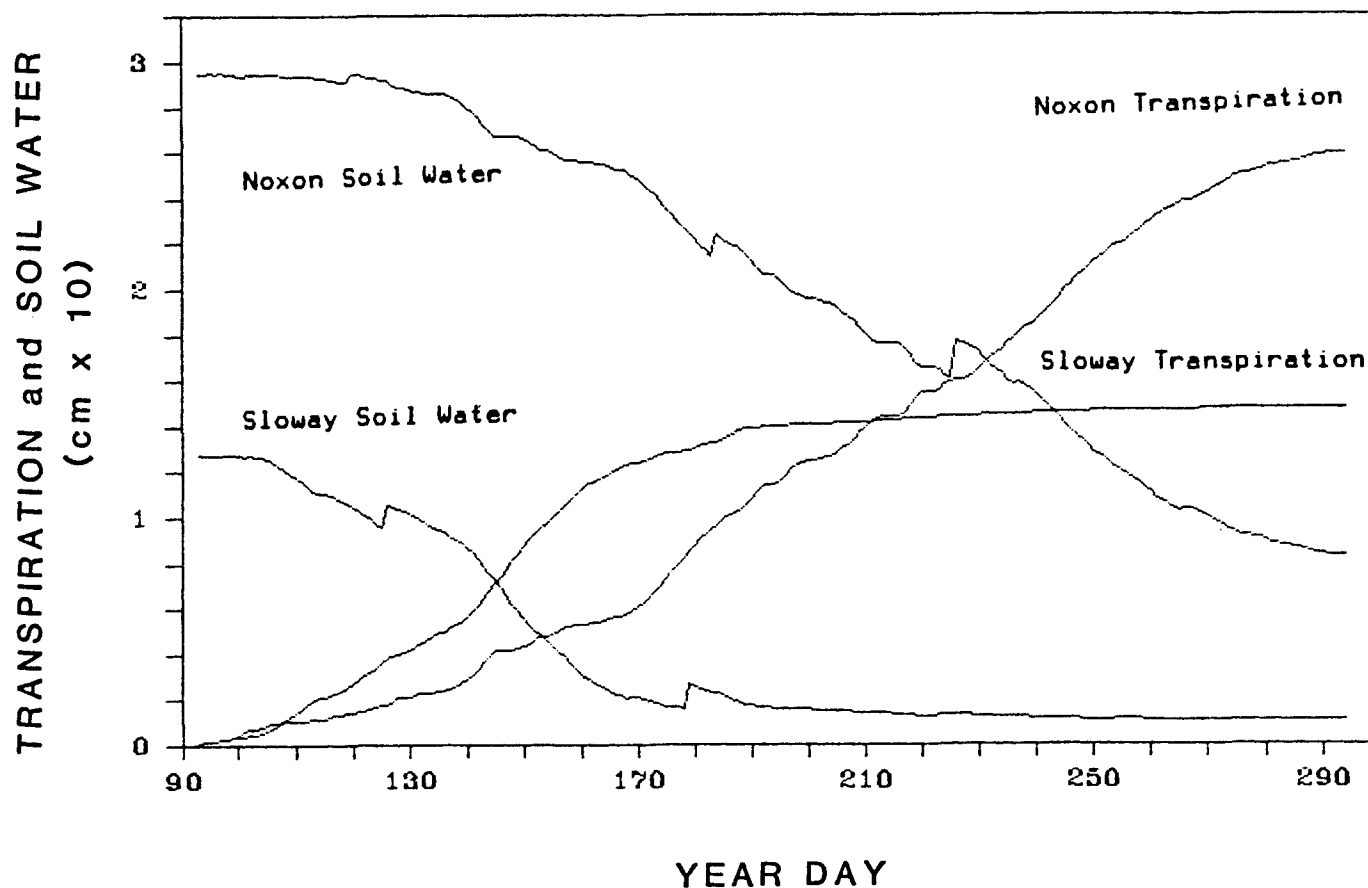
FIGURE 7. The trend of soil water depletion and transpiration predicted by DAYTRANS-C, at Sloway and Noxon, indicating the interaction between temperature and water availability. Sloway had higher spring temperatures and so transpired more rapidly early in the season. However, depletion of soil water caused the virtual cessation of transpiration and photosynthesis.

APPENDIX A

SITE	PRECIPITATION	FIELD CAPACITY	WATER HOLDING CAPACITY	SNOWPACK WATER CONTENT
SLOWAY	40.6 cm	12.8 cm	9.1 cm	3.2 cm
EDITH	33.8	18.8	12.8	1.8
PLAINS	45.7	16.4	11.5	3.8
SORREL	33.8	23.5	19.2	1.8
TROY	64.3	21.6	13.9	5.3
NOXON	77.5	29.6	17.7	6.5