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Use of Climatic Water Balance Metrics as Site Productivity Predictors

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Use of Climatic Water Balance Metrics as Site Productivity Predictors

By

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Use of Climatic Water Balance Metrics as Site Productivity Predictors

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Estimates of long-term forest site productivity are required to inform multiple forest management objectives including growth and yield assessments, silvicultural planning, and biomass/carbon projections. Estimates traditionally have been quantified in the form of site index by measuring the average height-age relationships of dominant and codominant trees or using regional site index equations. Site index implementation requires that trees are free from suppression and that height growth results from the integration of the biological determinants of growth. While useful in even-aged stands, early age height growth suppression is common in uneven-aged forest structures making existing site indices difficult to assess. Additionally, the individual biological determinants of growth are not identified and do not provide a basis for site index to be mapped across the landscape or predicted under alternative climate scenarios. This research aims to characterize the major physiographic and climatic determinants of growth.

We obtained site index estimates for 203 ponderosa pine, 343 Douglas-fir, 232 lodgepole pine and 99 western larch trees throughout the state of Montana using regional equations (Milner 1992). Terrain descriptors (slope, aspect and elevation), climate normals (min/max temperatures, vapor pressure deficit), and climatic water balance (actual evapotranspiration and deficit) were derived for each site index tree at various resolutions (list range of resolutions ). Regression analysis was performed using a hierarchy of terrain, climate and mixed models. Slope, aspect, and elevation were able to explain approximately half the variation in site index for ponderosa pine, lodgepole pine and western larch. Geographically localizing the model increased the variance explained by the terrain models for all species except western larch. A simple climatic water balance interaction model (AET x DEF) was unable to explain much of the variation in site index. However, when climatic water balance was added to the terrain model the variance explained increased for all species. A biophysical model utilizing only water balance and climate variables explained more of the variation in site index than terrain based models for all species. Implications of spatial accuracy of the climatic data products and fine scale variation in tree data are discussed and recommendations for future research are provided.
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Chapter 1

Introduction

Forest managers across the world are charged with the responsibility of determining forest productivity in order to make ecologically sound management decisions. In North America, these decisions are commonly based on the method of estimating forest productivity by using site index curves indicating the average height of free growing dominant trees at a reference age. Site index is often utilized in growth and yield models for estimating future resources and forest structure, as well as for predicting future growth based on current management objectives (Cairns et al. 2003). Additionally, site index is needed to guide planting forecasts to ensure that well informed, economical investments are made (Briggs and Wickramasinghe 1990).

In order to accurately estimate forest productivity using site index, multiple conditions must be met including: 1) that dominant tree height increment is independent of stand conditions; 2) that dominant trees have not experienced suppression or other damage; and 3) that tree height is an effective integrator of the key biological determinants of growth (Weiskittel et al. 2011a). These conditions are not universally met under today’s forest management regimes. For example, the USDA Forest Service uses an ecological approach by managing forests using uneven-aged silvicultural methods to achieve forests that represent diverse, healthy, productive, and sustainable ecosystems (Guldin 1996). These methods also consider the combined needs of U.S. citizens and the environment and include ecosystem services such as recreation, wildlife
habitat, carbon sequestration, and water quality. Uneven-aged management has become a popular alternative to even-aged management because it allows foresters to follow two ecological paths that forested ecosystems would otherwise take in the absence of management: succession and disturbance. By allowing (or mimicking) succession to occur, complex age, and spatially heterogeneous canopy structures result. This causes near ubiquitous early height growth suppression and makes site index determinations a difficult task in uneven-aged stands.

Other, non-traditional attempts at productivity assessment include geocentric measures of productivity. These utilize quantifications of the physiographic and climatic profiles of a site to estimate forest productivity. Geocentric approaches have typically been based on spatial data products resolved at coarse scales (~1km²). Estimates of productivity derived from these data products are unable to distinguish among the myriad of microclimates that exist in complex terrain. As a result of coarse scale products, geocentric estimates of site productivity can be subject to considerable uncertainty.

Further complicating geocentric assessments of productivity, there is no agreement as to which properties of the soils, physiography, or microclimate most strongly influence long-term forest productivity. For example, Carmean (1975) enumerated multiple studies that indicate the importance of soil properties for determining site productivity, yet Monserud et al. (1990) provided evidence showing that soil properties across a large geographic region (western MT and ID) are only weakly correlated with site index. These contrasting results suggest that the size of the study area, data resolution and variability in soils may obfuscate relationships with measures of long-term productivity.

Until recently, spatially-resolved climate data have been unavailable for forested areas and previous climate profiles were small in scale and incomplete. To circumvent this issue
topography has been used as a surrogate for climate (e.g. with elevation gradients standing as proxies for temperature gradients or growing season variations). Now that technologies are available to directly measure or interpolate climate variables between meteorological stations, an understanding of the mechanisms by which climate affects tree productivity can be explored in greater detail.

Understanding the relationships between climate and long-term forest productivity is also important because of the current concerns regarding global climate change. Topographic features, such as aspect, cannot directly account for energy and water interactions in site productivity models – topographic variables can only indirectly cover these effects by the way in which they affect moisture and temperature through shading and orographic effects. In the northern hemisphere, northeast aspects receive the most shade, and southwest aspects the least, resulting in different energy and water profiles. Northeast aspects will have less of an atmospheric demand for water and will be able to retain more soil/snow water throughout the year mediating the effects of high energy inputs. The opposite is true for southwestern aspects.

Under alternative climate scenarios topographic variables can be expected to remain relatively constant. Temperature and precipitation patterns however, are predicted to change (Boisvenue and Running 2010) and as a result, site energy and water budgets will be modified. Now that climate variables can be measured or imputed for forested ecosystems, these measurements can be used to estimate climatic water balance metrics, potential evapotranspiration (PET), actual evapotranspiration (AET) and water deficit (DEF), that integrate a site’s energy and water budgets. The energy and water budgets, if correlated with site index, may contribute to better estimates of the productive potential of a forest site at the current time as well as under alternative future climate scenarios.
Integrated climatic water balance metrics, specifically AET, have shown a high degree of correlation with productivity, predominantly when the latter is measured in terms of periodic net primary productivity (NPP) (Rosenzweig 1968). However, their utility for estimating long-term forest productivity has not been established. If the relationship between climatic, physiographic, climatic water balance, and long-term forest productivity can be linked then estimates of productivity could be based on these plant relevant variables.

This study aims to use climatic water balance metrics and fine-scale physiographic information to predict variations in site index. The specific objectives of this project are (1) to review previous uses of topography, climate and climatic water balance for predicting forest productivity; and (2) to infer site index as a function of topography and climate variables estimated by current technology and models. Motivating these objectives are the following hypotheses. First, climatic water balance (AET and DEF) are biologically relevant variables that describe the site energy and water budgets actually sensed by plants. AET and DEF, as well as climate variables, should be able to explain more of the variation in dominant tree height growth than static topographic variables. Secondly, because AET is the simultaneous availability of water and energy and DEF is a measure of water stress, sites with larger values of AET will result in higher productivity values while sites with larger values of DEF will result in lower productivity measured as dominant tree height.
Chapter 2

Literature Review

2.1 History and Development of the Site Index Concept

Determining the productive capacity and site quality of a forest stand is fundamental to natural resource management and stewardship. Previous as well as current attempts to quantify forest productivity have relied on empirical evidence based on height/age relationships commonly known as site index. Site index is a direct phytocentric measurement that is defined by the realized or expected stand height at a given age of dominant (or dominant and co-dominant) trees which are free from previous suppression and injury. In a practical sense, the site trees are phytometers of the productive capacity of the land and are assumed to be an effective integrator of the key biological determinants of growth (Weiskittel et al. 2011a). While site index is based on assumptions and limitations that are sometimes violated, its ubiquity in forest management is well documented. A large portion of its popularity is due to its ease of implementation over other measures of productive capacity as well as to its historical precedent.

During the 18th century the first attempts to classify a forested site were geocentric in nature, having to do with soil texture and geographic position. These methods indexed sites into broad classifications such as “low-altitude clay soil of medium production for beech” (Skovsgaard and Vanclay 2008). It was only after years of forest production that sites were indexed by volume using “experience tables” which reflected typical stand development. Yet such tables were unable to be used to project future growth or determine the current volume of a
specific stand or site. Instead the tables were based on an assumed average or typical stand. A century later site classification indices were created based on the fact that mean stand height at a given age correlated with stand volume at the same age. This correlation was first scientifically identified in 1841, though it was not until 1877 that the first yield tables were created based on classifying site by stand height (Skovsgaard and Vanclay 2008). It is worth noting that the European methodology for site identification was based on experience with managed even-aged stands in which height growth is largely independent of stand density. North American foresters lacked this long-term experience and, though they enjoyed what seemed to be an inexhaustible resource, faced a broad diversity of stand types.

In the United States forest management as we know it today did not exist until the birth of the Forest Service in 1905. At that time volume yield tables – or other methods to measure forest productivity – did not exist for any of the native tree species. Over the next two decades there was considerable debate over how to measure productivity. Some forest scientists were inclined to adopt height growth, others volume growth, and still others advocated for vegetative site type classifications (Monserud 1988). Eventually volume production was recognized as the most suitable indicator of forest productivity, even though paucity of long-term data and a wide range of stand densities made accurate volumetric production assessments infeasible. Vegetative site type methods were eschewed since not enough information was known about the native plant species and compositions. This left height increment as the most reasonable metric based on the facts that i) volume increment is related to height growth, ii) height growth could be measured relatively easily, and iii) height growth of dominant trees was perceived to be largely independent of stocking level.
In 1923, the Society of American Foresters recommended that yield tables for well stocked stands be constructed using height as an index. Based on measurements from temporary plots using inferred stand height at an index age, Bruce (1926) developed stand yield tables based on a proportional guide curve method. This method did not rely on actual measurements of tree height growth but instead on the total height and total age of dominant and co-dominant trees throughout a forest region to obtain an overall average site index (Carmean 1975). The average height-age curve served as a baseline off of which growth rates on low or high quality sites were proportionally fitted. The technique was widely applied, but relied on the assumption that height growth patterns were the same for all site classes found throughout broad regions spanning multiple states (e.g. Missouri to Maryland, or Michigan to Georgia; Schnur 1937). The method was thus unable to recognize climatic regimes and environmental gradients existing at local scales.

It was not until the 1950s that forest managers were beginning to see large discrepancies between what the guide curve methodology predicted and what was actually realized. Monserud (1988) cites multiple examples of such discrepancies: Carmean (1956) found inaccurate predictions on well drained and imperfectly drained soil types; Daubenmire (1961) found large biases in ponderosa pine stands when habitat type was ignored; and Spurr (1952) and Curtis (1966) saw biases greater than 20 ft in height estimates on remeasured Douglas-fir plots. The evidence against the proportional curve method was building and foresters started to lean towards stem analysis as a means of measuring actual growth over time. Among other things, stem analysis techniques provided a means of estimating polymorphic guide curves for growth and yield modeling, relaxing the assumption that height growth proceeds at the same rates regardless of site index.
2.2 Assumptions Underlying the Site Index Concept

Today site productivity is most commonly assessed from field measures of tree height and age and the application of site index equations based on polymorphic height growth curves. Yet the site index concept rests on multiple assumptions that are often difficult to fulfill in practice. Even when suitable site trees are observable forest managers must realize that various tree, stand, and broader environmental conditions do affect dominant tree growth and thus the tree and stand level predictions of yield.

The most fundamental assumption of site index is that the height growth of dominant trees is a true indicator of site potential (Monserud 1984a). For this to hold, it is necessary to presume that height growth is not influenced by stand conditions such as stocking or site preparation (Monserud 1984a), is not modified over the long-term by genetic and environmental attributes (Monserud and Rehfeldt 1990), and is an effective integrator of all biological components that influence stand volume production (Weiskittel et al. 2011a). The extent to which these conditions hold is the subject of a significant amount of literature.

The assumption that site index is independent of stocking (density) has been shown to fail on sites at the extreme ends of density ranges. The most commonly cited case at the lower extreme is Spurr (1952). In study sites of white oak he showed that stands at low density were shorter than well stocked stands at the same age. At the other extreme, studies have indicated that over-stocked stands can actually stagnate growth (Alexander et al 1967, MacFarlane 2000). These studies provide evidence that height growth can be influenced by stand density and therefore site index may not be a practical indicator of productivity.

Another assumption underlying the utility of site index is that dominant tree height is correlated with stand volume in well stocked stands. This can hold in even-aged, single-species
stands. Unfortunately, many forests in the interior of the United States are composed of mixed-species and multi-cohort stands, except where trees have reestablished after a fire or another significant disturbance. Alternatively, due to different growth rates and shade tolerances, stands that initiate as even-aged (e.g. post-fire regeneration) might not culminate in even-age structures. This complicates forest productivity estimation in two ways: 1) the difference in growth rate and ability to persist sub-canopy will lead to suppression and 2) multi-species stands require decisions to be made regarding which species’ site index curves should be used to predict productivity. In this region, it is not uncommon to have multiple species of value on a site and thus choosing only one to be an indicator of productivity can be uninformative (Monserud 1988).

From a more practical standpoint, the estimation of site index requires accurate determinations of tree or stand age. Yet the initial height growth of site trees can be extremely variable and may be affected by such factors as animal, insect or frost damage and even suppression from inter-tree competition (Monserud 1988). Additionally, in some cases it can be impossible to determine age due to heart rot. Fortunately, most of this variability can be accounted for by assessing age at breast height in mature trees.

Other difficulties that arise when site index is considered for uneven-aged stand include: complications in suitable site tree identification, stand age determination, and a lack of data and experimentation from uneven-aged management regimes which could be used for validation (Peng 2000). Dominant trees in such stands typically have been suppressed at one point or another and have had to vie for dominant position in the canopy while succeeding through the phases of canopy development (Kimmins 2004). The ability for site index to be a good measure of productivity is determined by a species’ ability to release from suppression, a tree’s time since release and the species’ shade tolerance (Weiskittel et al. 2011a). Adjustments to tree age to
account for growth suppression becomes necessary when a dominant tree is unable to recover from release (Seymour and Fajvan 2001). Alternatively, empirical and process-based forest growth models such as PROGNOSIS (Stage, 1973 and Wykoff et al. 1982) and PP-MASAM (O’Hara 1996) can be implemented to estimate forest productivity when age is unknown.

Finally, the assumption that dominant tree growth trajectories are constant over time is another problem attributed to the site index. The construction and application of site index equations presumes that long-term climatic variation at a given site is negligible and will have no effect on long-term growth. Alluding to a dendrochronology study by Leahphart and Stage (1971), Monserud (1984) points out that the lowest period of observed growth was in the 1930s when normal yield tables were being constructed in the USA. This could be partly responsible for why the original site curves developed by Bruce incorrectly predicted height and volume growth. But more importantly, now it is known that long-term and directional changes in climate are occurring, their effects on tree and stand growth should be explicitly considered.

Other factors such as site preparation, soil compaction, loss of nutrients from intensive management, fertilization, and genetic improvement (or adaptation; Monserud and Rehfeldt 1990) can cause long-term growth rates to change over time. This illustrates that site index may be an inappropriate measure of productivity if it is linked to current tree height and age measurements and not to the micro-climatic and geographic features that ultimately condition tree growth.

Despite the underlying assumptions and limitations of site index it is the most widely employed measure of productivity in forest management. Over the course of almost a century there have been significant advances in the predictive power and precision of productivity based on this index. This is a result from the improvement in the methodology of garnering growth data
and the construction of polymorphic curves that reflect actualized tree growth via stem analysis. In addition, previous research has shown the importance of habitat type (Monserud 1984b), genetics (Monserud and Rehfeldt 1990), edaphic qualities (Monserud et al. 1990, and synoptic environmental factors (Klinka and Carter 1990) in determining the shape and height of site index curves. The desired resolution of the equation for implementation by forest managers ultimately depends on the financial feasibility and ability of foresters to collect the relevant data without error. Fortunately, for most regions, species-specific equations exist (e.g., Milner 1992), even if these have many and various conditions affecting how and where they can be applied.

Monserud (1984) suggests that the most important of these conditions relates to the field methodology used for constructing site index height/age relationships. The requirements for estimating a stand’s site index includes averaging 15-20 dominant and co-dominant tree heights that are representative of the stand while using the oldest tree to assess stand age. To obtain this representative sample and to minimize tree sampling error, stratification of sites by levels of precipitation, temperature and solar insolation or their proxies slope, aspect and elevation can be performed prior to selecting site trees (Carmean 1975). Averaging site index values or under-sampling tree heights have shown to bias estimates of site index. Intentionally misapplying these methods resulted in biases of 4-16 feet translating into a 30% overestimation in wood volume. This illustrates the importance of reviewing the appropriate field measurement protocols associated with equation development prior to implementing them to characterize the productivity of a given stand.

Many previous and current efforts have been made towards improving the utility and feasibility of site index estimation. It is without a doubt the most common measure of productivity today however, in many cases it falls short. Perhaps most importantly, it requires in
situ tree measurements. In order to address these limitations, alternative methods have been developed to estimate site productivity. These methods use edaphic, physiological, and climatic data that characterize a site as it relates to productivity. This information can either be obtained directly from the site or remotely sensed. Estimation of productivity is then carried out directly from calibrations against field measurements, or via the implementation of empirical or process based models of forest growth.

2.3 Geocentric Approaches to Characterizing Site Productivity: Edaphic Factors

Forest management spans a wide range of objectives from timber production to conservation. As stated in the previous section, estimating productivity via site index becomes impractical when forest stands deviate from an even-age structure leaving few trees free from previous suppression. In addition, in uneven aged forests stand age is largely irrelevant and the association between dominant height growth and stand volume accumulation breaks down. Yet productivity estimates are needed in order to make informed management decisions. In such cases, site productivity potential may be approached geocentrically by quantifying edaphic, physiographic, and climatic variables that condition forest productivity. However, this approach is not without its limitations. Productivity responses can be species specific (e.g. shade tolerant species will respond differently to solar radiation than shade intolerant species) and broad, multispecies generalizations remain elusive. Also, as discussed below, interactions among geocentric variables – measured and unmeasured - are often important.

The use of edaphic properties as predictors of site productivity potential has been extensively documented (Carmean 1975). Since soil is the medium for plant life and has the ability to cycle nutrients and hold water, it is recognized that its properties should be strong
predictors of plant productivity. Some of the soil properties most commonly related to productivity are parent material (Rospopina et al. 2011), water availability, nutrient levels, bulk density (Grigal 2009), and water holding capacity as well as texture, depth and type of bedrock (Ritchie and Hamann 2008). Surrogates for soil forming processes such as slope position, elevation (Monserud et. al 1990), aspect (Carme 1975) and synoptic climate (Klinka and Carter 1990) are also of importance when considering relevant variables for predicting forest productivity.

Productivity and soil associations have been found to vary as a result of high spatial variability in soil properties within forest stands and over large geographic regions. The most common method to ascertain the form and strength of these associations is to analyze the soil properties (e.g. texture, water holding capacity, nutrient concentrations etc.) at a site and perform stem analysis to obtain a site index value. Using statistical regression methods, the soil properties over many different profiles are then associated with different values of site index to arrive at empirical relationships. If a wide range of site index is not sampled then it is likely that only weak statistical correlations will be observed. The size of the study area is also important in that if it is too small then results will have a limited domain of application while if the study area is too large it is possible that large-scale variability in, say, parent materials will obscure fine-scale effects on forest productivity.

The geographic range sampled in conjunction with the number of sites sampled was found to be a primary factor contributing to weak correlations between soil properties and site index in a study in northern Idaho and western Montana (Monserud et. al 1990). Another potential factor cited by the authors of that study was that the true causes of site productivity were not measured. For instance, water availability was measured in the form of moisture
holding capacity. Moisture holding capacity is the difference in plant available water held by soil particles between field capacity and wilting point. This may be an irrelevant measure because the wilting point is synonymous with plant death and does not truly reflect the available water for growth. In addition, the timing of water availability, which was not considered, could be of great importance. Regardless, it was concluded by Monserud et al. that the high costs associated with collecting soil attributes was not justified in terms of their predictive ability.

Another study by Klinka and Carter (1990) in coastal British Columbia was able to distill much stronger relationships between soil properties and forest production potential. The sample points for that study were distributed across three climatic regimes, five soil moisture regimes, and five soil nutrient regimes. Soil nutrient regimes and synoptic climate were treated as factor variables in regression models that explained 84% of variation in site index. The study also indicated that inaccurate and incomplete measurements of continuous variables relating to moisture and soil nutrient regimes as has been done in previous studies (Monserud et. al 1990) reduced the amount of variation explained; more variation was explained when soils were broadly classified into distinct moisture and nutrient categories.

2.4 Geocentric Approaches to Characterizing Site Productivity: Physiographic Factors

Beyond soils, numerous physiographic measures have been used to estimate forest site productivity. Slope, aspect, latitude, longitude and elevation are the most commonly studied physiographic metrics (Weiskittel et al. 2011a). Broadly, in the northern hemisphere, forest productivity increases from southwest facing slopes to northeast facing slopes (Carmean 1975, Coble et al 2001). Slope position also is broadly associated with productivity, with the lower positions typically being more productive due to deeper soil profile (Carmean 1975). Latitude
and longitude have also been directly compared against forest productivity. Monserud et al (1990) found that longitude ($R^2=0.12$) was a useful predictor, with productivity increasing from eastern to western study sites. It was concluded that this was due in part to orographic lifting over mountainous terrain in the Pacific Northwest, coupled with the direction of prevailing winds (from the Pacific). In contrast, latitude did not appear related to productivity in that study. This is likely due to the fact that large differences in latitude are needed to bring about the kinds of changes in forest productivity noted on many global maps of NPP and GPP (Zhao et. al 2005). In regard to latitude, the greatest levels of productivity are generally observed in the equatorial, tropical rainforests with decreases at higher absolute latitudes as a result of solar energy limitations (Littell 2008) and seasonality.

The role of elevation gradients in conditioning species occurrence and productivity is well known throughout the ecological literature. These effects were first noted by the founder of modern biological nomenclature, Carl Linnaeus. In more recent studies, Monserud (1988 and 1990) credits elevation as being one of the most important factors affecting forest productivity. When combined with habitat type (an ecological classification) it explained 39% of the variance of site index, with productivity decreasing with elevation. The decrease in productivity is not driven by elevation per se but from the fact that ecosystems at higher elevations have lower temperatures and in some cases less precipitation. As a consequence the growing seasons are shortened compared to lower elevations resulting in reduced production (although lower elevation sites are associated with reductions in productivity due to an increase evaporative demand).
2.5 Geocentric Approaches to Characterizing Site Productivity: Climatic Factors

Direct physiographic models of productivity are generally based on crude measurements or indirect empirical relationships and do not address the mechanisms driving productivity. Instead they use topographic proxies for variations in climate (Chen et al. 1999). For example, aspect, elevation and topography alter radiation, temperature and soil moisture budgets, which in turn directly impact plant communities.

While lack of climate data has been problematic in the past, there now exist high resolution climate data sets derived from increased meteorological observations and improved computational/physical models of mesoclimatic processes. Climate variables can now be estimated at ≤1 km² resolutions from an extensive network of stations and climate models (e.g. DAYMET (Thornton et al 2012), PRISM (Daly et. al 1994), and WxTopo (Oyler and Running 2013)). In addition, the development of inexpensive micrometeorological recording sensors has facilitated the acquisition of highly resolved (spatially and temporally) meteorological data to monitor specific study areas or identify small-scale topographic influences (Holden et al. 2011 and 2013). These technologies permit the use of actual or estimated climate metrics to be used to assess the biophysical characteristics that drive productivity through direct associations or via process based models.

For example, utilizing climate data obtained from the Alberta Climate Model, Monserud et al. (2006) were able to evaluate the utility of various climate variables in terms of predicting lodgepole pine site index. The study used 16 different climate variables including mean annual temperature (MAT), mean annual precipitation (MAP), growing season precipitation, among other descriptors of temperature and seasonal ranges. Climate regime was calculated for each of
the 1145 plots and regression analysis was used to predict site index using thin-plate smoothing spline surface fitting techniques. The first and second best predictors were Julian date when growing degree days reached 100 \( (r=-0.52) \) and growing degree days \( (r=0.50) \), respectively. Adding additional variables did not improve the model. Unlike other studies (McLeod and Running 1987, Littell et al 2008, and Corona 1998), statistically significant correlations between site index and MAP, growing season precipitation, and winter duration were absent, suggesting that water was not the primary limiting factor in Alberta lodgepole pine ecosystems.

Alternatively, a study in British Columbia utilized PRISM (Parameter-elevation Regressions on Independent Slopes Model) climate data to predict site index for lodgepole pine, Douglas-fir and interior spruce (Nigh et al. 2004). Site index for lodgepole pine was best predicted from number of frost free days, annual heat: moisture index, and temperature differential \( \text{RSME}=1.581 \text{ m} \); Douglas-fir was best predicted using mean annual temperature, annual heat: moisture index, and temperature differential \( \text{RSME}=2.883 \text{ m} \); and interior spruce, was best predicted using mean temperature of the warmest month but was found to have a RSME=3.153 m indicating that the species relationship to climatic variables was weaker than the two other species.

The latter study also assessed site index changes due to climate change scenarios. The model indicated that all three species would become more productive with increasing temperature \( (1.6 \text{ m for every } ^\circ\text{C}) \) and increased precipitation would enhance site index for lodgepole pine and Douglas-fir. The estimated changes in site index for lodgepole pine, Douglas-fir, and interior spruce are 2.5 m, 4.5 m, and 3.5 m, respectively. These positive responses are indicative of the primary limiting factors within the ecosystems. In interior Douglas-fir stands, changes were most sensitive to increases in precipitation indicating water
limitation; lodgepole pine increases were sensitive to increases in temperature indicating energy limitation. No conclusion was drawn for interior spruce. This study as well as others (Monserud et al. 2006, McLeod and Running 1987, and Corona et al. 1999) emphasized the importance of water and energy budgets as they relate to productivity and that their presence is fundamental when constructing site index prediction models using climate variables.

2.6 Geocentric Approaches to Characterizing Site Productivity: Process-Based Methods

Technological advances in satellite remote sensing and modeling have provided new ways in which forest productivity can be assessed instantaneously in the form of gross primary production (GPP) and net primary production (NPP). GPP is the carbon fixing ability of an ecosystem and includes not only sequestered carbon (NPP=GPP-respiration) but also the carbon needed for maintenance (i.e. respiration). Estimates are generated using satellites to measure the fractions of photosynthetically active radiation which is then translated using algorithms to determine GPP and NPP. Process based models such as 3PG (Landsberg and Waring 1997) can also produce estimates of GPP and NPP. These estimates are generated using parameters such as radiation use efficiency, water use efficiency, carbon balance, and partitioning. While ranges of complexity of model inputs exist, estimates rely on the accurate measurement of several site factors.

The relationships among GPP, site index (SI), and climate was evaluated in a recent study by Weiskittel et al. (2011b) by comparing different estimates of GPP (MODIS and 3PG) and Douglas-fir SI against a host of climate variables. When SI and GPP were compared only a moderate correlation was obtained (Spearman rank correlations of 3PG-0.65 and Modis-0.70). Regression relationships between climate variables and the three measures of productivity
indicated that across a large portion of the Pacific and interior northwest the degree of winter coldness, availability of moisture in the growing season, and range of temperature fluctuations explained the bulk of the variation in site index (R²=0.68). Improvements in the models were observed by increasing the number of climate variables to 7 (R²=0.78). The results indicate that a better relationship exists between site index and a small set of climate variables than between estimates of GPP derived from MODIS and 3PG. Due to process models being difficult to parameterize and requiring multiple layers of input data, estimating productivity would be more practical by applying climate variables to predict SI.

Another study comparing process modeling outputs with SI examined the relationships of leaf area index, SI, available water index, and gross photosynthesis to volume growth of ponderosa pine stands in western Montana (McLeod and Running 1987). Site index and leaf area index were derived from empirical measurements while available water index and gross photosynthesis were based on computer generated (DAYTRAN-C) quantifications of the biophysical factors that influence productivity. All indices were strongly correlated with volume growth (R²>0.93); however, the ability to interpret the effects of available water index was difficult considering it did not account for timing of precipitation events nor evaporative demand. DAYTRAN-C comparisons of gross photosynthesis across the 6 sites indicated that sites with less water availability experience moisture stress in mid June (even though temperature stayed in optimal ranges for growth) halting photosynthesis. Photosynthesis continued until mid-August which then water limited sites experience moisture stress while the remaining non-water limited stands continued at potential rates until temperatures were no longer conducive to growth. This is similar to the previously mentioned studies to the degree that at large geographic scales sites are either water limited or they are energy limited.
Using a water balance approach to study limiting factors across a longitudinal ecological gradient, Littell et al. (2008) compared Douglas-fir growth among sites from the Olympic Peninsula, WA to the eastern Rocky Mountain front, MT. Limiting factors were assessed with climate data and the variable infiltration capacity (VIC) hydrological model which interpolates temperature and precipitation data as well as soil and vegetation properties. The model is also parameterized to estimate hydrological variables such as evapotranspiration, snow water equivalent, and soil moisture. The study used dendrochronological methods to assess the relationship between tree ring widths and regional climatic and biophysical determinants of growth. It indicated that across the transect, water limitation was the most important factor related to growth; temperature was less important. In particular the water balance deficit of the prior growing season was correlated with tree growth. The strongest correlations were observed in the Idaho Panhandle National Forest; weakest in the Olympic National Forest. These two sites differ in regional climate, mostly in moisture availability and temperature ranges, and reflect the fact that water becomes a more of a limiting factor as distance from maritime influences increases.

The mechanism driving reductions in growth stem from ecophysiological responses to interactions between plant, soil, and atmosphere. In particular, vapor pressure deficit, the difference between the amounts of water in the air vs. the amount in the leaves, controls stomatal resistance. As temperature increases latent heat is removed by water transpiration through the stomates. When the amount of plant available soil water is reduced due to this and other evaporative demands, the stomates close to reduce plant water stress, effectively halting photosynthesis and reducing growth potential. Other adaptations that reduce growth but mitigate water stress include reducing leaf area though abscission, which will affect carbon assimilations.
when water balance normalizes and hydraulic redistribution when water below the root zone is available (Littell et al. 2008). Ultimately, the increase in growing season water balance deficit driven by climate is directly related to a decrease in growth potential.

2.7 Geocentric Approaches to Characterizing Site Productivity: Climatic Water Balance

The geocentric approaches to estimating forest productivity described above require no direct tree measurements for application, yet are able to quantify productivity by integrating other site properties that influence growth. These approaches are thus useful when a site is devoid of trees, when other conditions favorable to the measurement or use of site index are not met, or when productivity must be mapped over large areas. The underlying theme of these studies is that growing season energy, water availability and the interactions between the two are essential for predicting productivity. Variables related to temperature and water, as well as their derivatives, are consistently utilized throughout the literature. However, not one specific set of variables are used consistently to describe these relationships (Stephenson 1990). A probable reason given by Stephenson (1998) is that in most studies water and energy have been treated as if they act independently on plants when in fact they act jointly. For plants to use energy for photosynthesis water must be available. Likewise, for plants to use water then energy must be available. Another reason given is that many of these studies infer local moisture conditions by using topographic moisture scalars. Stephenson (1998) shows that sites with similar scalar values vary greatly in productivity due to differing plant responses to evaporative demands and available water. That is to say that the evaporative demand sensed by a plant on a south facing slope is different than the evaporative demand sensed by a plant on soils with a low water holding capacity. This difference is expressed in plant phenology as well as plant productivity.
In addition, areas of similar insolation, temperature and seasonality can support different vegetation types due to differences in precipitation timing. To better describe the relationships between plant productivity and the abiotic environment a climatic water balance model is suggested. This approach estimates potential evapotranspiration (PET), actual evapotranspiration (AET), deficit, and surplus to arrive at biologically relevant estimates that can be directly linked to productivity (Rosenzweig 1968).

Estimates of water balance variables are typically made for a standard crop, such as a continuous field of grass, so that current vegetation characteristics do not influence site comparisons. Holding these vegetation characteristics constant, potential evapotranspiration is the evaporative demand of the atmosphere at any given time. It is the maximum amount of evapotranspiration that can occur at a site given unlimited soil moisture. Actual evapotranspiration, by contrast, is the amount of evapotranspiration from soil evaporation and plant transpiration given soil water available to the reference crop. Following from these definitions, deficit is the difference between potential evapotranspiration and actual evapotranspiration and surplus is the water supply exceeding potential evapotranspiration (Fig 2.1; adapted from Stephenson 1998).
Estimates of these climatic water balance variables can be derived from a multitude of equations ranging from simple to complex (Fisher et. al 2011). Potential evapotranspiration has at least 50 different equations to estimate its value (Fisher et. al 2011). Due to only requiring a few, easily measured variables the simplest PET equations are temperature based. Of these temperature based models, the Thornthwaite equation is the most commonly used in ecological studies even though Thornthwaite advised others not to use this equation beyond the U.S. Midwest. In addition to mean temperature, this equation has an advantage over other temperature based models due to its incorporation of day length, an implicit variable for the amount of insolation at a given site, which can be linked to the duration of photosynthesis (Fisher et. al 2011). However, the temperature based equations have been shown to inaccurately predict PET in tropical regions and in deserts which limits application to more temperate regions.
Equations using radiation inputs are also used to estimate PET and AET. The energy balance model states that: net radiation = the heat stored in soil + heat stored in biomass + sensible heat + AET. Since a certain amount of energy is required to make the phase transfer of water from a liquid state to a vapor state, AET can then be solved for if the other variables are known. More complex models, such as the Priestly-Taylor method, use net radiation and empirical constants to estimate PET. While some of these models have been successful in estimating PET these models do not account for the atmospheric demand of water which may result in a bias.

To account for this discrepancy, combination equations have been developed that integrate radiation and temperature models with atmospheric drivers of evapotranspiration. The most widely used models are Penman (1948) and Penman-Monteith (1965). In addition to incorporating temperature and radiation, these equations use wind speed and vapor pressure deficit (VPD) to estimate PET. Vapor pressure deficit is the difference between the amounts of water vapor an air mass can hold at a given temperature minus the amount that is currently held. When the difference is large, the atmosphere draws more water via evapotranspiration. Wind speed is indicative of the rate of atmospheric mixing and resistance. Penman’s original equation was modified by Monteith in 1965 to include such variables as stomatal and aerodynamic resistance of vegetation. The opening and closing of stomates can be regulated by pressure gradients within vegetation to counteract a high atmospheric demand. Doing so effectively decreases or halts transpiration depending on the gradient of pressure. The aerodynamic resistance term, or surface roughness, accounts for the wind passing through and over a canopy which creates turbulence and drives evapotranspiration by creating wind eddies and increase water loss from the stomates and water that has been intercepted by the canopy. Forest stands
are tightly coupled to the atmosphere, due to a high degree of surface roughness, and are subject
to evapotranspiration through VPD and aerodynamic resistance.

The Penman-Monteith equation is the most widely used technique for estimating PET,
though it has several important limitations. It was initially designed for agricultural crops which
are typically homogenous in species and height. This homogeneity makes the equation easy to
implement since only one set of aerodynamic and stomatal resistance coefficients are needed.
When it is applied to vegetation with multiple species and vertical structure it becomes difficult
to produce aerodynamic and stomatal resistance coefficients for all species. When these
parameters are known, with the addition of soil moisture, then AET can be estimated but when
they are not then only reference crop PET can be estimated. Raupach and Finnigan (1988)
showed that incorrect values for aerodynamic and stomatal resistance biased estimates of
Penman-Monteith PET.

AET and PET for extant vegetation systems can also be directly measured and/or
estimated remotely. Direct measurements, in order of increasing difficulty include: pan
evaporation, sap flow, lysimetry, and eddy covariance (Fisher et. al 2011). While pan
evaporation is the simplest of the methods it does not account for transpiration and also
introduces an artificial setting for evaporation to take place (i.e. the metal pan). Sap flow
systems measure the amount of water flow in the tree by measuring heat initially introduced at a
lower portion of the stem. When the heated stem water passes along another sensor the length
over the time produces a rate at which water is flowing thorough the xylem. This measurement
needs to be scaled up to canopy level and in doing so can introduce error. Similar to pan
evaporation, lysimeters measure the change in soil weight over a time period to estimate
evapotranspiration but is extremely difficult to accurately construct and operate. Lastly, eddy
covariance, using precision instrumentation, measures the amount of water vapor in the air, wind speed and direction is able to calculate a covariance term which is then translated into the AET for a particular area. While eddy covariance towers are very accurate in estimating water balance metrics in areas of flat terrain, homogenous vegetation, and steady atmospheric inputs (i.e. temperature, wind, humidity) they do not do well over complex terrain and structures (Baldocchi 2003). In order for accurate assessment in these situations, measurements of atmospheric storage, divergence, and advection must be accounted for to produce a reliable estimate of AET.

Remote sensing of water balance metrics uses eddy covariance data to calibrate regional (Nagler et. al 2013) and global measurements (Mu et. al 2007) of water balance metrics for current vegetation. Nagler et al. (2013) used 5 years of eddy covariance tower data as well as PET from a reference crop to develop an algorithm for calculating AET using Moderate Resolution Imaging Spectrometer (MODIS). The resulting algorithm was able to predict AET across crops and riparian areas ($r^2=0.73$) and for 5 irrigation districts ($r^2=0.89$). Global estimates of ET using data from eddy covariance towers and MODIS were modified by adding VPD and temperature constraints on stomatal conductance, substituting leaf area index for canopy conductance, using Enhanced Vegetation Index and adding a soil evaporation calculation. The results produced global spatial patterns of evapotranspiration similar to spatial patterns of NPP and GPP.

The relationship between productivity, either measured in NPP or GPP, and AET was first established by Rosenzweig (1968) but in a very crude form by basing estimates of AET on latitude and mean temperatures. Now with technological advances AET can be directly measured and or remotely sensed and relationships between AET and primary production (NPP)
can now be mapped. Understanding the role of NPP in forest ecosystems is currently of great importance as it relates to the global carbon budget and anthropogenic climate change (Dixon et. al 1994, Melillo et. al 1996). Field measurements have been shown to underestimate NPP due to the absence of a standardized method and confusion concerning which measurements are needed (Clark et. al 2001). In addition, the difficulties of measuring belowground biomass have been shown to be important. For landowners and managers wanting to exploit the relationship between productivity and climatic water balance, it is likely that direct measurement of NPP would be cost prohibitive and infeasible in addition to providing a measure of instantaneous production as oppose to a prediction of future site productivity. Instead, a relationship between water balance metrics and common measurements of forest attributes (e.g., volume or basal area growth) would be more informative in terms of wood production, planting forecasts, and predicting growth responses in light of global warming.

Wicramasinghe (1988) and Briggs and Wicramasinghe (1990) modeled the impacts of effective evapotranspiration (AET of forest stands during the growing season) on both basal area growth and volumetric growth for 11 and 38 sites, respectively. Using an analog of the water balance model (Precipitation=groundwater + Δ storage + runoff + AET), they were able to establish a relationship between effective ET and potential growth by summing AET over each month of the growing season. AET was calculated using a ramp function (France et. al 1981) in which AET was set equal to PET when soils were at 67-100% of field capacity. Reduction in soil moisture beyond 67% caused AET to linearly decline at the rate equal to the slope of the function. The average variability explained by this ET model was 60% and 50% for volume and basal area growth, respectively, across 38 study sites. Some of the unexplained variation was attributed to the absence of information on soil rooting depth, drainage and nutrient status in the
model. However, this model would be applicable for broad generalizations to forest productivity.

As it has been stated above, climatic water balance calculation can be performed by utilizing a variety of methods. A consideration for the type of climatic data available and the ecological system of study is necessary when attempting to calculate these metrics. Fisher et al. (2011) compared the Thornthwaite, Priestley-Taylor, and Penman-Monteith PET equations for 11 sites across a latitudinal transect from northern Alaska to southern Brazil and showed equation differences of 25% over the transect. Equation selection should therefore be determined by the spatial and temporal nature of data and study sites. For example, if the estimation of PET is for a small forested lot then using climatic data at >1km² could result in a biased estimate in heterogeneous terrain. If seasonality plays a role in climatic water balance then metrics should be calculated in a way that reflects this. An understanding of the environmental parameters governing the equations is also needed. For example, it cannot be expected that a temperature-based equation would produce unbiased estimates of PET at the arctic or that the Thornthwaite PET equation, which assumes continuous vegetation, would unbiasedly estimate PET in deserts.

While equation estimates diverge across a global scale they can also diverge at the forest ecosystem level. Fisher and others (2005) compared five PET equations to measurements of actual evapotranspiration recorded at an AmeriFlux site above the forest canopy. Each model predicted a different level of PET. As expected, all equations over-predicted towards the end of summer due to soil water deficit. An added soil moisture function improved estimates by multiplying PET by the relative amount of water in the soil. Others have produced similar predictive models by modifying a PET equation to account for soil moisture (O’Brien 1993,
Field et. al 2005). In addition, the 2005 study by Fisher et al. found that the simple Priestly-Taylor model coincided with AET when the empirically derived constant for soil moisture (α) was modified to reflect actual soil moisture. Because this equation is easier to parameterize it has been suggested for application at larger spatial scales.

Climatic water balance metrics are able to integrate the two most important rate-limiting drivers of photosynthesis, energy and water. Previous studies have shown that biological activity is highly correlated with these metrics. As trees, forests, and biomes capture radiant energy and sequester carbon they produce the byproducts of oxygen and water. Thus where data required to calculate climatic water balance metrics are available, an investigation of their utility as predictors of potential forest productivity should provide a significant contribution.
Chapter 3

Methods

3.1 Tree and Site Characterization

The following sections describe the methods used for estimating and obtaining site index, topographic variables, climate variables, and climatic water balance variables. Tree measurements were assessed in the field while topography and climate were estimated using the models described below.

3.1.1 Tree Measurements

Individual tree site index (SI) data used in this analysis were collected throughout the state of Montana as part of a previous research project for the Montana Department of Revenue (Zuuring et al. 2008). A total of 1,355 trees comprised of ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta* var. *latifolia*) and western larch (*Larix occidentalis*) were selected using a stratified list-sampling protocol based on precipitation zones within ecoregions throughout the state of Montana. For each individual tree the following information was recorded: geographical coordinates (latitude and longitude), species, diameter at breast height (DBH), total height, crown ratio, and stand basal area per acre. Breast height age was determined by extracting a tree core from the tree at breast height 4.5 ft (1.37 m). The core was evaluated for evidence of previous growth suppression. Depending on the degree of suppression inferred, each tree was ranked in terms of suitability for SI estimation,
with classifications including unsuitable, potentially suitable, and suitable. Individual-tree 50 year SI values were computed using species-specific equations developed for western Montana (Milner 1992) using breast height age and total height.

### 3.1.2 Topographic Features

Topographic data were obtained for each individual SI tree from the National Elevation Dataset (NED) produced by United States Geological Survey (Gesch 2007). The NED is comprised of multiple digital elevation models (DEM) and includes digital representations of cartographic information in raster form which can be obtained at various resolutions. For this study latitude and longitude coordinates were used to extract elevation, aspect, and slope at 30 m × 30 m resolution. Topographic position index (TPI), a measure of the topographic position (valley, ridge, etc.), was also calculated for each SI tree from the NED. This index is produced by an algorithm which compares the elevation of a DEM cell to the mean elevation of a specified neighborhood around that cell (Weiss 2001). For this study, neighborhoods were specified using 150 m and 300 m buffers. Positive TPI values indicated that the cell containing the SI tree(s) was at least as elevated as its surroundings (e.g. upper slopes and cliff edges). Negative values indicated that the trees were positioned lower in elevation than at least some neighboring pixels (e.g. lower slopes and narrow valley bottoms) and zero values indicated either that the mean elevation of the surrounding neighborhood was similar to that of the SI cell or that slope was constant (e.g., flat or mid-slope conditions).
3.1.3 Climate Variables

Monthly climatological averages for minimum, maximum, and dew-point temperatures, as well as precipitation were obtained from PRISM (Parameter-elevation Regression on Independent Slopes Model; Daly et al. 2008) at a 30 arc-second grid size (~800 m × 800 m grid cells) for the period 1971-2000. PRISM combines temperature and precipitation data from i) the National Weather Service Cooperative Observer Program, ii) the Natural Resources Conservation Service snowcourses, iii) Snow Telemetry (SNOTEL) stations, and iv) the USDA Forest Service Remote Automated Weather Stations (RAWS). Meteorological observations for this network of weather stations are then interpolated to estimate climate variables across the landscape while considering meteorological phenomena associated with mountainous terrain (e.g. temperature inversions, topographical barriers, air flow, and cold air drainage; Daly et al. 2008).

Due to its physiological importance in the evapotranspiration process, vapor pressure deficit (VPD) was calculated using an equation developed by the Food and Agriculture Organization (Allen et al. 1998). First, for each month the saturation vapor pressure was calculated using the equation:

\[
es_s = 6.11 \times 10^{(7.5 \times T_{max})/(237.3 + T_{max})}
\]

where \(e_s\) is the saturation vapor pressure and \(T_{max}\) is the monthly maximum temperature. Then the same equation was used substituting dew-point temperature (Tdew) for \(T_{max}\) to estimate the actual vapor pressure \((e_a)\). The difference between \(e_s\) and \(e_a\) is VPD (measured below in kPa) and is a measure of the drying force of the atmosphere and thus of the force driving the movement of water from the soil through the plants to the atmosphere (Chapin et al. 2011).
To calculate climatic water balance, the Penman-Monteith equation (Monteith 1965) was used to calculate potential evapotranspiration (PET) of a reference crop, also as described by Allen et al. (1998) and implemented by Dobrowski et al. (2012). Subsequently, a hydrological model incorporating snowpack effects and STATSGO soil available water holding capacity (Soil Survey Staff 1995) was used to quantify annual actual evapotranspiration (AET) and deficit (DEF). The form of the Penman-Monteith PET equation is:

$$\text{PET} = \frac{\Delta (R_n - G) + \rho_a c_p \frac{e_s - e_a}{r_a}}{\Delta + \Upsilon \left(1 - \frac{r_s}{r_a}\right)} \tag{2}$$

where $R_n$ is the net radiation (MJ m$^{-2}$ day$^{-1}$), $G$ is the soil heat flux (MJ m$^{-2}$ day$^{-1}$), $\rho_a$ is the mean air density at constant pressure (kg m$^{-3}$), $c_p$ is the specific heat of air (MJ kg$^{-1}$ °C$^{-1}$), $\Delta$ is the slope of the saturation vapor pressure temperature relationship, $\Upsilon$ is the psychrometric constant ($0.665 \times 10^{-3} \times$ atmospheric pressure as a function of altitude; kPa °C$^{-1}$), and $r_a$ and $r_s$ are the aerodynamic and bulk surface resistances (s m$^{-1}$), respectively.

The aerodynamic resistance in eq. [2] is calculated by solving the following:

$$r_a = \frac{\ln \left(\frac{z_m - d}{z_{om}}\right) \ln \left(\frac{z_h - d}{z_{oh}}\right)}{K^2 u_z} \tag{3}$$

where $z_m$ and $z_h$ are the height of heat and humidity measurements (m), respectively, $d$ is zero-plane displacement (0.67× reference crop height; m), $z_{om}$ is the roughness length governing the momentum transfer (0.123× reference crop height; m), $z_{oh}$ is the roughness length governing the transfer of heat and vapor (0.1 $z_{oh}$), $K$ is von Karman’s constant (0.41) and $u_z$ is wind speed (m s$^{-1}$). In turn, bulk surface resistance in [2] is calculated as

$$r_s = \frac{r_l}{LAI_{active}} \tag{4}$$
where \( r_l \) is the bulk resistance of a single leaf and \( \text{LAI}_{\text{active}} \) is the active (sunlit) leaf area index (leaf area : soil surface area). For a reference crop of grass, Allen et al. (1998) indicated that \( \text{LAI}_{\text{active}} = 0.5 \) LAI where, in general, \( \text{LAI} = 24h \) for crop height \( h \) (m). Given that a standard reference crop is 0.12 m tall and has a single leaf bulk surface resistance of 100 s m\(^{-1}\) the following is the solved equation for reference crop bulk stomatal resistance:

\[
rs = \frac{100 \text{ s m}^{-1}}{0.5 \times 24 \times 0.12} = 70 \text{ s m}^{-1}
\]  

[5]

Dobrowski et al. (2012) found that several modifications of the PET equation [2] were required in order to produce reliable estimates of reference crop evapotranspiration that allow for the effects of cold temperature and snow. The first modification was to account for the increased reflectivity of solar radiation when snow was present. By adjusting albedo from its reference value of 0.23 to 1.0, \( R_n \) was modified for winter months. The second modification required was to the bulk resistance term \( r_s \) since stomates are closed at low temperatures and cannot transpire. The new modification scaled the bulk resistance of one leaf as shown in the equation below for calculating bulk surface resistance:

\[
rs^* = \frac{1}{k_s(T)} \frac{r_l}{\text{LAI}_{\text{active}}}
\]  

[6]

where \( r_s^* \) is the modified bulk surface resistance, \( r_l \) is the bulk surface of a single leaf, \( k_s(T) \) is the scaling parameter, and \( \text{LAI}_{\text{active}} \) is the leaf area index of the active canopy. The scalar, \( k_s(T) \), is defined by three parameters: low temperatures \( (T_l) \), optimal temperatures \( (T_o) \), and high temperatures \( (T_h) \). Specifically,

\[
k_s(T) = b_3 \ (T - T_l) \ (T_h - T)^{b_4}
\]  

[7]
where \( b_3 = [(T_0 - T_l) (T_h - T_0)]^{b_4} \) and \( b_4 = (T_h - T_0)/(T_h - T_l) \). When mean monthly temperatures were below 5˚C this scalar was used to adjust bulk stomatal resistance but when the mean temperature exceeded 5˚C then \( r_s \) was calculated as described by Allen et al. (1998). In addition to the equations described above, the water balance model used the inputs given in Table 3.1 (adapted from Dobrowski et al. 2012) to estimate annual AET and DEF.

### Table 3.1 Sources of input data for calculating annual actual evapotranspiration and deficit.

<table>
<thead>
<tr>
<th>Input</th>
<th>Source</th>
<th>Spatial resolution</th>
<th>Timestep</th>
</tr>
</thead>
<tbody>
<tr>
<td>30 yr Normal Maximum Temperature</td>
<td>PRISM(^a)</td>
<td>800 m × 800 m</td>
<td>monthly</td>
</tr>
<tr>
<td>30 yr Normal Minimum Temperature</td>
<td>PRISM(^a)</td>
<td>800 m × 800 m</td>
<td>monthly</td>
</tr>
<tr>
<td>30 yr Dewpoint Temperature</td>
<td>PRISM(^a)</td>
<td>800 m × 800 m</td>
<td>monthly</td>
</tr>
<tr>
<td>Precipitation</td>
<td>PRISM(^a)</td>
<td>800 m × 800 m</td>
<td>monthly</td>
</tr>
<tr>
<td>Elevation</td>
<td>NED DEM(^b)</td>
<td>30 m × 30 m</td>
<td></td>
</tr>
<tr>
<td>Radiation</td>
<td>SOLRAD(^c)</td>
<td>30 m × 30 m</td>
<td>monthly average</td>
</tr>
<tr>
<td>soil available water capacity (AWC)</td>
<td>STATSGO(^d)</td>
<td>800 m × 800 m</td>
<td></td>
</tr>
<tr>
<td>Wind</td>
<td>NLDAS-2(^e)</td>
<td>30 m × 30 m</td>
<td>monthly average</td>
</tr>
</tbody>
</table>

\(^a\) Daly et al. 2010 obtained from PRISM Climate Group in August 2010  
\(^b\) National Elevation Dataset Digital Elevation Model (Gesch 2007)  
\(^c\) Shade corrected solar radiation (Flint and Childs 1987)  

Summarizing, to estimate atmospheric demand for water, 800 m × 800 m grid cells of reference crop PET were calculated using the climatic inputs from Table 3.1 for each site tree location. PRISM precipitation and soil available water capacity were used to estimate precipitation and the water budget for each site. When the atmospheric demand was equivalent to the PRISM precipitation and available soil water then AET was assumed equal to PET; where the atmospheric demand was greater than the estimated supply AET was set equal to that supply and a positive water deficit (DEF > 0) resulted. The formula for adjusting evapotranspiration as a
function of available soil moisture to obtain AET is provided by Allen et al. (1998). The equation uses a dimensionless transpiration reduction factor ($K_s$):

$$AET = PET \times K_s$$  \hspace{1cm} \text{[8]}$$

where $K_s = \frac{TAW - Dr}{TAW - RAW} = \frac{TAW - Dr}{(1 - \rho) TAW}$, TAW is the total available water, RAW is readily available water, Dr is the root depletion zone, and $\rho$. As water is depleted by evapotranspiration, the water content of soils decreases and soil water tension increases. This results in a lower water potential gradient between the plants roots and the atmosphere. At a crop dependent threshold, a function of species-specific characteristics such as stomatal control and rooting depth, water stress occurs and the evaporative demand of the atmosphere (PET) cannot be achieved. Thus the amount of water stress (as measured by $K_s$) changes over time and requires updated estimates of Dr. These can be calculated as:

$$D_{r,i} = D_{r,i-1} - (P_i - RO_i) - I_i + ET_{c,i} + DP_i$$  \hspace{1cm} \text{[9]}$$

where $D_{r,i}$ is root zone depletion at the end of day $i$ (mm), $D_{r,i-1}$ is water content in the root zone at the end of the previous day (mm), $P_i$ is precipitation on day $i$ (mm), $RO_i$ is runoff from the soil surface on day $i$ (mm), $I_i$ is day $i$ soil infiltration (mm), $ET_{c,i}$ is crop evapotranspiration on day $i$ (mm), and $DP_i$ is water loss out of the root zone by deep percolation on day $i$ (mm).

Figure 3.1 shows the relationship between $K_s$, TAW, RAW. Water-stress adjusted values for reference crop evapotranspiration were based on monthly data and aggregated to produce annual estimates of AET and DEF for this study.
3.1.4 Growing Season Radiation

Solar radiation is an important determinant of forest productivity because it provides the radiant energy required to drive photosynthesis and evaporation. It can be a scarce resource in some forest strata, leading to competition, or it can be overabundant, and lead to plant stress, excessive heat loads, and water scarcity. Because of its importance in driving productivity, researchers have developed multiple methods for estimating solar radiation. The model used for this project was developed by Flint and Childs (1987) and accounts for the scattering and reflection effects of the atmosphere, the effects of shading caused by mountainous terrain, and the topographic profile of the receiving surface (i.e. slope and aspect). From this model growing season radiation was calculated by aggregating daily radiation values (MJ m⁻² day) during the growing season months April-October.

Figure 3.1 Water stress (Ks) and available water content.
3.2 Modeling Variation in Site Index

Prior to model development, relationships between SI and the available topographic and climatic variables were assessed graphically using scatterplots and spline curve fits. The goal of this initial analysis was to determine whether the marginal effects of the predictors were linear or nonlinear. A hierarchy of regression models was then used to assess the degree of variation in SI explained by the topographic and climatic predictors. The models were species-specific and ranged from simple forms, incorporating as few as two covariates, to more complex models utilizing inter-related sets of geocentric and climatic predictors. The simplistic models were then combined to assess if adding more complexity to the model would explain additional variation in SI. Furnival’s Index (Furnival 1961) was used as a diagnostic to determine if linear or log-linear forms of SI were required. The model form with the lowest index values was selected as the best expression of the covariates’ influence on SI.

3.2.1 Geocentric Models

The most basic geocentric regression model used only latitude and longitude to predict SI for each of the species:

\[ SI = b_0 + b_1 \text{Latitude} + b_2 \text{Longitude} + \varepsilon \]  \hspace{1cm} [10]

where the error terms \( \varepsilon \) are assumed to be independent across trees with constant variance.

A second model using the predictor combinations suggested by Stage and Salas (2007) was also used in this study. Specifically, Stage and Salas (2007) suggested modeling the joint effects of slope (S), elevation (E), and aspect (A) on productivity using a set of 11 marginal and multiplicative combinations of these variables resulting from the mathematical expansion of
\[ SEA_{11} = S \left[ 1 + \cos(A) + \sin(A) \right] \left( 1 + \ln(E) + E^2 \right) + E + E^2 + \varepsilon \]  

[11]

Utilizing this set of terms, SI was modeled as

\[ SI = b_0 + SEA_{11} b + \varepsilon \]  

[12]

where SEA\(_{11}\) is a 11-column matrix containing the variables from the expansion of eq. [11] and \(b\) is a 11 \(\times\) 1 vector of coefficients. Many of the individual terms on the right hand side of eq. [11] are correlated, but the overall form aims to account for the interactive effects that these topographic attributes can have on forest productivity. Additionally, they have the ability to account for the varying effects that aspect can have on productivity at the extremes of elevation (or what is termed a “phase shift” by Salas and Stage 2007). At lower elevations, north and northeast aspects are generally optimal in terms of growth for most tree species because they offer cooler temperatures and are often shaded as a result of the <90° sun angle. With increasing elevation, this interaction causes north aspects to become less productive due to energy limitation (as a result of relatively lower temperatures). At the same time, southern and western aspects at higher elevation experience a decrease in temperatures (lower evaporative demand) and still receive long durations of incoming solar radiation (as a result of the <90° sun angle) making these aspects more favorable to growth.

Although Stage and Salas (2007) used expression [11] for predicting forest presence and absence and mean annual increment and not to predict SI, they noted that model [12] can be used to assess whether or not models incorporating the direct effects of radiation, precipitation, and temperature are better suited for forest productivity predictions. This was done by adding Universal Transverse Mercator (UTM) coordinates to the equation to localize the effects of \(SEA_{11}\). Similarly, the topographically-based model [12] was supplemented in this study by adding latitude, longitude and TPI300.
\[ SI = b_0 + SEA_{11} b + b_{13} \text{Latitude} + b_{14} \text{Longitude} + b_{15} TPI300 + \epsilon \]  \[13\]

Furthermore, the residuals from model [13] were plotted against the available climate variables (temperature, VPD and climatic water balance metrics) to determine if any of the unexplained variation in SI could be attributed to the direct effects of climate.

### 3.2.2 Biophysical Models

Following a similar approach as was used for the development of geocentric models, a simple biophysical model was first fit using only AET and DEF and their interaction:

\[ SI = b_0 + b_1 \text{AET} + b_2 \text{DEF} + b_3 \text{AET} \times \text{DEF} + \epsilon \]  \[14\]

Model [14] was supplemented by adding the topographically based model [13] to determine if additional variation could be explained by the BIOTOP model:

\[ SI = b_0 + SEA_{11} b + b_1 \text{AET} + b_2 \text{DEF} + b_3 \text{AET} \times \text{DEF} + b_{16} TPI300 + \epsilon \]  \[15\]

To provide an initial evaluation and ranking of the potential explanatory power of the full set of available climatic variables (monthly minimum, maximum, and dew point temperatures; monthly VDP; growing season radiation; mean growing season maximum temperatures; and aggregated growing season VPD) all were used to predict SI using a random forest (RF) (Breiman et al. 1984 and Breiman 2001) algorithm. Specifically, the entire climate data set was evaluated by RF by building 200 regression trees and testing 3 variables at each node. Since the dataset contains multiple monthly temperatures and VPDs, RF was also implemented to determine the most important temperature and VPD based on the importance rating derived from the RF algorithm. This was performed by iteratively fitting models until either one temperature or one VPD was observed to add the most explanatory power to the model. For example, if after the RF simulation a temperature was determined to have the most explanatory power then
all other temperatures were removed and the selected temperature remained in the dataset. Continuing with this example, another simulation would be subsequently run using the remaining variables (in this case all monthly VPD’s, all other climate variables, and the one temperature variable) and the VPD with the highest importance rating was then selected.

The results from the random forests models were used to specify a model using a consistent set of predictors for all species. This set of variables included AET, DEF, growing season mean maximum temperature (GSTMAX)

\[
\text{GSTMAX} = \frac{1}{8} \sum_{i=3}^{10} T_{\text{max}(i)}
\]  

[16]

aggregated growing season VPD (GSVPD),

\[
\text{GSVPD} = \sum_{i=3}^{10} \text{VPD}(i)
\]  

[17]

and growing season radiation (where \( T_{\text{max}(i)} \) and \( \text{VPD}(i) \) are maximum temperature and VPD in calendar month \( i \)). The conditional effects of each of these predictor variables on SI were assessed using partial response curves from generalized additive models (GAM). After appropriate specifications of each predictor’s effects were determined, multiple linear regression models (MLR) and generalized linear models (GLM) with log and square root link were used to compare model fit.

### 3.2.3 Model Performance and Comparison

All statistical analysis was performed using the R statistical package (R Core Team 2013). Root mean squared error (RMSE) was used to determine overall model error

\[
\text{RMSE} = \sqrt{\frac{1}{N} \sum (y_{\text{obs}} - y_{\text{pred}})^2}
\]  

[18]
where $y_{\text{obs}}$ is the observed tree SI, $y_{\text{pred}}$ is the predicted tree SI from a given model, and the sum extends over all $N$ trees. Adjusted $R^2$ was used to compare the goodness of fit of the various models

$$\text{Adjusted } R^2 = 1 - \frac{(1 - R^2)(N - 1)}{N - p - 1}$$

[19]

where $R^2$ is the coefficient of determination of a model, and $p$ is the number of predictors in that model. The signs and magnitudes of the estimated effects associated with individual variables were also assessed to determine whether or not they were biologically reasonable. Linearity, normality, and constant variance were assessed graphically from residual plots.

For the models incorporating the topographic covariates suggested by Stage and Salas (2007), tests of significance were not applied to the individual predictor variables. Such models used aspect, elevation, and slope several times in various transformations and product terms. As such, the individual predictors are not linearly independent, and their effects cannot be interpreted or tested in isolation because they appear in multiple terms in the model. Additionally, multicollinearity existed within the climate dataset requiring the biophysical models to be evaluated using the same methods for SEA$_{11}$ models. The multicollinearity in this dataset differed for these variables because it was the result of the inherent characteristics of the climate dataset (e.g. high temperatures are associated with high VPD) as opposed to the possible combinations and transformations of slope, elevation, and aspect. Otherwise, contributions of individual predictors or sets of predictors to the explanatory power of the model were assessed using analysis of variance (ANOVA) F-tests of differences in the regression sums-of-squares.

Model abbreviations and incorporated predictors are given in Table 3.2.
Table 3.2. Predictor variables used in each model.

<table>
<thead>
<tr>
<th>Predictors</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Elevation</th>
<th>Slope</th>
<th>AET</th>
<th>DEF</th>
<th>TPI</th>
<th>GST</th>
<th>GSVPD</th>
<th>Equation</th>
</tr>
</thead>
<tbody>
<tr>
<td>LatLon</td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>[10]</td>
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<td>SEA11</td>
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<td></td>
<td></td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>[12]</td>
</tr>
<tr>
<td>SEA11 (LatLon)</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td></td>
<td>x</td>
<td></td>
<td></td>
<td></td>
<td>[13]</td>
</tr>
<tr>
<td>AETDEF</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>[14]</td>
</tr>
<tr>
<td>BIOTOP</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>[15]</td>
</tr>
<tr>
<td>BIOPHY</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Chapter 4

Results

4.1 Distributions of Tree and Site Characteristics

The following sections provide the results of the distributions and characteristics of the tree-level site index, topographic, climate, and climatic water balance data obtained using the methodology described in section 3.1.

4.1.1 Tree Characteristics

Of the 1,355 SI trees collected throughout the state of Montana there were 877 that fell within the requisite parameters (i.e. free of past suppression) in terms of the suitability index. This resulted in data sets of 203 ponderosa pine, 343 Douglas-fir, 232 lodgepole pine, and 99 western larch SI trees. Maps of the SI tree distributions are found in Fig. 4.1 and Table 4.1 provides summary statistics for each species.

SI trees of all four species were located across western Montana and all but western larch were found in central Montana as well. Across those regions lodgepole pine and Douglas-fir had relatively uniform spatial distributions compared to ponderosa pine which was concentrated in two distinct groups, one in western Montana and another in central Montana. Due to its restricted geographic range and preference for mesic sites, western larch was found exclusively
in northwestern Montana where the influence of mountainous terrain, prevailing winds, and maritime influence result in greater precipitation.

![Image of tree locations](image1.png)

**Figure 4.1** SI tree locations for each species; map scale is approximately 1cm:164 km.

<table>
<thead>
<tr>
<th>Species</th>
<th>Mean (m)</th>
<th>Minimum (m)</th>
<th>Maximum (m)</th>
<th>Standard deviation (m)</th>
<th>Trees (number)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ponderosa pine</td>
<td>16.2</td>
<td>2.2</td>
<td>27.4</td>
<td>4.9</td>
<td>203</td>
</tr>
<tr>
<td>Douglas-fir</td>
<td>14.9</td>
<td>3.0</td>
<td>23.8</td>
<td>3.7</td>
<td>343</td>
</tr>
<tr>
<td>Lodgepole pine</td>
<td>15.5</td>
<td>7.3</td>
<td>24.7</td>
<td>3.0</td>
<td>232</td>
</tr>
<tr>
<td>Western larch</td>
<td>19.5</td>
<td>12.8</td>
<td>27.7</td>
<td>2.7</td>
<td>99</td>
</tr>
</tbody>
</table>
Averaged tree level SI ranged from 19.4 m for western larch to 14.9 m for Douglas-fir, with an overall average of 16.5 m. The variability within SI for each species was large with ponderosa pine having a the largest standard deviation of 4.9 m and western larch having the smallest amount of variation (standard deviation 2.7 m). Figure 4.2 shows a decline in estimated SI with tree age for ponderosa pine and Douglas-fir. This may in part reflect past management practices, with highly productive sites being managed more intensively than less productive sites resulting in the presence of more older, slower growing trees. Alternatively, it may represent an unaccounted source of error in the SI equations of Milner (1992).

Figure 4.2. Scatterplots of SI and breast height age. Sets of trees in individual (species-specific) 800 m × 800 m climate pixels are highlighted in red.
Tree height and breast-height age distributions for each species are summarized in Table 4.2. Mean breast-height age ranged from 57 to 72 years across the species, but variation in individual tree ages was large, with lodgepole pine having the greatest spread (standard deviation of 25 years). While some trees are close to the reference age of 50 years, no observations were made at the reference age. Instead, SI (past or future height at breast-height age 50 years) has been estimated using the region-specific equations of Milner (1992). Overall 361 SI values have been projected forward and 516 projected into the past using these equations.

Table 4.2. Site Index tree breast height age (years) and height (m) summary statistics per species.

<table>
<thead>
<tr>
<th>Species</th>
<th>Breast Height Age</th>
<th></th>
<th></th>
<th></th>
<th>Plots (number)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean (years)</td>
<td>Minimum (years)</td>
<td>Maximum (years)</td>
<td>Standard deviation (years)</td>
<td></td>
</tr>
<tr>
<td>Ponderosa pine</td>
<td>57</td>
<td>25</td>
<td>108</td>
<td>19</td>
<td>203</td>
</tr>
<tr>
<td>Douglas-fir</td>
<td>64</td>
<td>20</td>
<td>140</td>
<td>21</td>
<td>343</td>
</tr>
<tr>
<td>Lodgepole pine</td>
<td>62</td>
<td>21</td>
<td>120</td>
<td>25</td>
<td>232</td>
</tr>
<tr>
<td>Western larch</td>
<td>72</td>
<td>20</td>
<td>101</td>
<td>18</td>
<td>99</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Species</th>
<th>Height</th>
<th>Minimum (m)</th>
<th>Maximum (m)</th>
<th>Standard deviation (m)</th>
<th>Plots (number)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ponderosa pine</td>
<td>16.8</td>
<td>7.3</td>
<td>33.5</td>
<td>4.6</td>
<td>203</td>
</tr>
<tr>
<td>Douglas-fir</td>
<td>16.8</td>
<td>6.4</td>
<td>32.3</td>
<td>4.6</td>
<td>343</td>
</tr>
<tr>
<td>Lodgepole pine</td>
<td>16.2</td>
<td>5.8</td>
<td>27.4</td>
<td>4.6</td>
<td>232</td>
</tr>
<tr>
<td>Western larch</td>
<td>23.8</td>
<td>12.5</td>
<td>35.1</td>
<td>4.9</td>
<td>99</td>
</tr>
</tbody>
</table>

Figure 4.2 illustrates the maximum variation in site index for each species that occurred within individual PRISM pixels by highlighting groups of individual trees that fell in the same 800 m × 800 m areas. For example, there are 6 ponderosa pine trees in a single PRISM pixel that have breast height ages ranging from 32-54 years, heights ranging from 10.4-14.9 m, and estimated SI values ranging 13.1-21.1 m. Similarly, there are 8 Douglas-fir trees within one
pixel that have breast height ages ranging from 55-140 years, heights ranging 8.8-17.4 m, and estimated site indices from 2.9-11.7 m. Single-pixel ranges of estimated SI for lodgepole pine and western larch range from 18.8-24.8 m and 19.5-25.1 m, respectively.

### 4.1.2 Topographic Distributions

Summary statistics for aspect, elevation and slope for each species are in Table 4.3. SI trees are also plotted with respect to aspect and elevation in Figure 4.3 and are shaded according to estimated SI (darker points having a larger value of SI). Ponderosa pine SI trees were primarily sampled on south and western aspects at lower to mid elevations which is consistent with habitat and range descriptions (Stuart and Sawyer 2001, Arno and Hammerly 2007). Douglas-fir SI trees were measured throughout the ranges of aspect and elevation and no relationship with topography was evident. Lodgepole pine SI trees were observed at the upper ranges of elevation (also consistent with ecological distributions) and occupied all aspects. However, more lodgepole SI trees were sampled on south facing aspects. Western larch SI trees were selected predominantly on north and south facing aspects at mid elevations and on low to moderate slopes. Overall, the majority of SI trees were selected on 0-30% slopes and at elevations ranging 1050-2000 m. More Douglas-fir SI trees were measured on the steepest slopes.

Topographic position index 150 (TPI150) values for all four species ranged from -31 to 30 with an overall mean of 0.32. TPI300 values ranged from -82 to 72 with an overall mean for all four species of -1.4. Although wide ranges of topographic complexity were sampled, the distributions were largely symmetric and trees were concentrated closer to conditions matching midslope, saddle, or flat terrain (TPI ≈ 0).
Table 4.3 Distributions of SI trees across aspect, elevation, and slope classes by species.

<table>
<thead>
<tr>
<th>Topographic position</th>
<th>Ponderosa Pine</th>
<th>Douglas-fir</th>
<th>Lodgepole Pine</th>
<th>Western Larch</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Aspect (degrees)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>316 to 45 (N)</td>
<td>37</td>
<td>91</td>
<td>58</td>
<td>43</td>
</tr>
<tr>
<td>46 to 135 (E)</td>
<td>19</td>
<td>76</td>
<td>55</td>
<td>16</td>
</tr>
<tr>
<td>136 to 225 (S)</td>
<td>86</td>
<td>113</td>
<td>81</td>
<td>31</td>
</tr>
<tr>
<td>226 to 315 (W)</td>
<td>61</td>
<td>63</td>
<td>38</td>
<td>9</td>
</tr>
<tr>
<td><strong>Elevation (m)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>750 to 1049</td>
<td>27</td>
<td>31</td>
<td>0</td>
<td>6</td>
</tr>
<tr>
<td>1050 to 1349</td>
<td>108</td>
<td>83</td>
<td>8</td>
<td>28</td>
</tr>
<tr>
<td>1350 to 1649</td>
<td>61</td>
<td>101</td>
<td>37</td>
<td>58</td>
</tr>
<tr>
<td>1650 to 1949</td>
<td>7</td>
<td>77</td>
<td>51</td>
<td>6</td>
</tr>
<tr>
<td>1950 to 2249</td>
<td>0</td>
<td>31</td>
<td>108</td>
<td>1</td>
</tr>
<tr>
<td>2250 to 2549</td>
<td>0</td>
<td>20</td>
<td>28</td>
<td>0</td>
</tr>
<tr>
<td>Species Mean</td>
<td>1274</td>
<td>1552</td>
<td>1926</td>
<td>1422</td>
</tr>
<tr>
<td>Species SD</td>
<td>202</td>
<td>380</td>
<td>290</td>
<td>216</td>
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<tr>
<td><strong>Slope (%)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>00 to 10</td>
<td>53</td>
<td>35</td>
<td>38</td>
<td>19</td>
</tr>
<tr>
<td>11 to 20</td>
<td>55</td>
<td>40</td>
<td>45</td>
<td>15</td>
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<tr>
<td>21 to 30</td>
<td>54</td>
<td>93</td>
<td>58</td>
<td>24</td>
</tr>
<tr>
<td>31 to 40</td>
<td>14</td>
<td>59</td>
<td>45</td>
<td>19</td>
</tr>
<tr>
<td>41 to 50</td>
<td>15</td>
<td>38</td>
<td>26</td>
<td>19</td>
</tr>
<tr>
<td>51 to 60</td>
<td>7</td>
<td>41</td>
<td>12</td>
<td>1</td>
</tr>
<tr>
<td>61 to 70</td>
<td>5</td>
<td>12</td>
<td>6</td>
<td>1</td>
</tr>
<tr>
<td>71 to 80</td>
<td>0</td>
<td>23</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>81 to 90</td>
<td>0</td>
<td>2</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Species Mean</td>
<td>22</td>
<td>35</td>
<td>28</td>
<td>27</td>
</tr>
<tr>
<td>Species SD</td>
<td>15</td>
<td>19</td>
<td>16</td>
<td>15</td>
</tr>
</tbody>
</table>
Figure 4.3  Polar plots of the distribution of SI trees across aspect and elevation by species. Trees with larger values of SI are indicated with darker symbols and concentric circles indicate elevation contours of 500 m. Shown in red are the same sets of trees highlighted in Fig. 4.2.
The elevations and aspects of individual site trees also varied within 800 m × 800 m PRISM pixels (Fig. 4.4). For example, in one climate pixel, ponderosa pine trees ranged from 206° to 234° in aspect. In another pixel, Douglas-fir trees ranged in elevation from 1745-1782 m and had a range of aspect from 86° to 160°. The terrain variability per pixel is consistent throughout the dataset for each species and is a result of overlaying an 800 m × 800 m PRISM grid over continuously changing and sometimes extreme physiography.

Figure 4.4 Examples of the variation in aspect, elevation, and SI values for individual trees within 800 m × 800 m PRISM pixels. Note that axes scales vary by species, and that the trees shown are those highlighted in Fig. 4.2.

It is also interesting to note that pixels containing trees with similar aspects and elevations sometimes exhibit considerable variability in SI values. In the ponderosa pine pixel of Fig. 4.4, SI values differ 8.1 m over 3 trees on a southwest aspect that differ in elevation by only 6 m. The Douglas-fir pixel contains a group of trees at essentially the same aspect and that differ in elevation by 37 m and in SI by 8.8 m. Lodgepole pine has two trees with the same elevation
(1985 m) and aspect (309°) but differ in SI by 6 m. This is also present in the western larch data where within a single pixel 5.7 m differences in SI can be observed for trees with similar topographic profiles. This variation in SI within PRISM pixels will ultimately have an impact on the predictive ability of climatic and topographic variables derived at different resolutions.

Species-specific relationships between SI and elevation are plotted in Fig. 4.5. Lodgepole pine SI had the strongest linear correlation with elevation (r = −0.35) and Douglas-fir exhibited the largest variability in SI given elevation. Correlations of elevation with SI in ponderosa pine, Douglas-fir, and western larch were 0.32, −0.32, and −0.34, respectively.

Trigonometric transformations of aspect were made to represent north polarity [cos(aspect) increases as aspect approaches 0° or 360°] and east polarity [sin(aspect) increases as aspect approaches 90°E from either direction]. Weak positive correlations of SI with cos(aspect) existed for both western larch (r = 0.26) and lodgepole pine (r = 0.22) but were negligible for ponderosa pine (r = 0.18) and Douglas-fir (r = 0.04). Douglas-fir SI had a weak negative relationship with sin(aspect) but this was negligible for all other species (r < 0.10). For all species except for western larch, decreases in SI were observed on steeper slopes (though there was limited data from western larch trees on steep slopes; see Table 4.3). Ponderosa pine exhibited higher productivity on flat terrain and on slopes greater than 30%.

Correlations between geographic location and SI were generally strongest when the former was measured by longitude. Ponderosa pine SI had the strongest linear correlation with longitude (r = -0.62) and Douglas-fir the second strongest (r = -0.46). Lodgepole pine SI had only a moderate (and positive) correlation (r = 0.29) while western larch had a weak negative correlation (r = -0.21). The only species that exhibited a correlation between SI and latitude was lodgepole pine (r = -0.29).
Figure 4.5 SI and elevation for each species. Shown in red are the same trees highlighted in Fig. 4.2.
4.1.3 Climate Profiles

Distributions of annual climate water balance metrics, 30-year normal monthly maximum temperatures and 30-year normal VPD are displayed in Figs. 4.6- 4.8. Mean and range values differed for all species. The sites with ponderosa pine SI trees had the largest mean values of maximum temperature, VPD, and water deficit (DEF) among all four species and also the lowest mean value of AET. For these trees the atmospheric demand was relatively high and the sites were drier on average than those for the other species. Douglas-fir trees were selected over a larger range of climate and those sites had the second highest mean values for temperature, VPD, and deficit (but the second lowest mean AET value). Douglas-fir was also selected at the sites that had the highest mean maximum temperatures (29.5°C) of all four species. Lodgepole pine and western larch were generally selected in habitats that were more energy limited such as those at higher elevations and on north facing slopes, respectively. The energy limitation in lodgepole pine habitats is most likely due the shortened growing season that is common at higher elevations. It is not surprising then that the selected lodgepole pine trees were on sites with the lowest deficits, temperatures and VPD values. The lodgepole pine sample did have the second highest mean AET which may be attributable to snow ablation replenishing water supply throughout the majority of the growing season. Western larch were selected on sites that had the largest mean AET value but came second to lodgepole pine in lowest mean deficits, temperatures, and VPD values.
Figure 4.6 Distributions of actual evapotranspiration and deficit for each species. (PP=Ponderosa Pine, DF=Douglas-fir, LP=Lodgepole Pine, WL=Western Larch).

Figure 4.7 Distributions of growing season mean monthly maximum temperatures for each species. (PP=Ponderosa Pine, DF=Douglas-fir, LP=Lodgepole Pine, WL=Western Larch).

Figure 4.8 Distributions of growing season mean vapor pressure deficits (VPD) for each species. (PP=Ponderosa Pine, DF=Douglas-fir, LP=Lodgepole Pine, WL=Western Larch).
The relationships between AET or DEF and the various terrain variables were strongest in the case of elevation for ponderosa pine, lodgepole pine, and western larch and negligible for aspect and slope. AET values across the ponderosa pine sites had a strong positive relationship with elevation \((r = 0.60)\) while strong negative relationships existed across the lodgepole pine \((r = -0.48)\) and western larch \((r = -0.51)\) sites. The relationship between AET and elevation across the Douglas-fir sites was nonlinear, but weak. DEF and elevation were negatively correlated for all species. The correlation was very strong over the ponderosa pine sites \((r = -0.70)\) but moderate correlations across the other samples \((r \leq -0.40)\).

AET and DEF relationships were negative for ponderosa pine, Douglas-fir, and western larch but positive for lodgepole pine although weakly correlated \((r =0.17)\) (Fig. 4.9). Ponderosa pine and Douglas-fir AET had the strongest correlation with DEF \((r = -0.84\) and \(r = -0.69\), respectively) and western larch was moderately correlated \((r = -0.42,\) ). AET responses to both temperature and VPD were negative for both ponderosa pine and Douglas-fir and positive for western larch and lodgepole pine (Fig. 4.10; Note: VPD on x-axis shows similar response and is not provided). DEF for all species had a strong positive correlation with both VPD and maximum temperatures \((r > 0.70)\) (Figure 4.11; Note: VPD on x-axis shows similar response thus figure is not provided).

Figure 4.12 shows the highly correlated relationship between maximum temperature and VPD \((r >0.97\) for all species) although the data a constrained. Both temperature and VPD decreased with increasing elevations (Fig. 4.13; elevation and VPD shows similar response and is not provided) at an averaged environmental lapse rate of 5.7 °C for every 1000 m gained in elevation.
Figure 4.9 AET and DEF scatterplot with smoothers.
Figure 4.10 AET and August maximum temperature scatterplot with smoothers.
Figure 4.11 DEF and August maximum temperature scatterplot with smoothers.
Figure 4.12 August vapor pressure deficit and August temperatures scatterplot.
Figure 4.13 August maximum temperature and elevation scatterplot with smoothers
SI exhibited a positive relationship with AET for all species (Fig. 4.14). Ponderosa pine and lodgepole pine SI had the strongest linear correlation with AET (r = 0.48), while western larch and Douglas-fir SI displayed only weak positive associations with AET (r = 0.31 and r = 0.24, respectively). Western larch and lodgepole pine SI trees do not span as broad a range of AET as the ponderosa pine and Douglas-fir sites, constraining the ability to estimate or interpolate SI beyond current observations. Variability of SI values within the previously identified 800 m × 800 m PRISM pixels are also highlighted in Figs. 4.14-4.15.

Deficit and SI relationships were different for all four species (Fig. 4.15). Ponderosa pine SI has a strong negative correlation with DEF (r=0.63) and this sample spanned sites with the highest values of deficits among all four species. Douglas-fir SI responds positively as deficit increases to approximately 400 mm yr⁻¹ and subsequently declines leading to a very weak linear correlation (r = -0.08). Interestingly, western larch site index responds positively to deficit while lodgepole pine responds negatively. This could indicate that the selected lodgepole pine site index trees also occurred in sites that were water limited. Lodgepole pine SI has only a moderate positive correlation with deficit (r=0.38) while no relationship is apparent for western larch (r = 0.04).
Figure 4.14 Site index and annual actual evapotranspiration scatterplot with smoothers. Shown in red are the same trees highlighted in Fig. 4.2.
Figure 4.15 Site index and annual water deficit (DEF) scatterplot with smoothers. Shown in red are the same trees highlighted in Fig. 4.2.

SI responses to late season maximum temperatures and VPD were also different for all species (but each species showed similar responses to each of the two metrics because of the strong relationship between late season temperatures and VPD (Fig. 4.19). Ponderosa pine SI has a strong negative relationship with both August maximum temperatures and August VPD ($r = -0.43$ and $r = -0.41$, respectively). Conversely, site index in the Douglas-fir and lodgepole pine trees responded positively to both August temperatures and August VPD ($r = 0.35$ and $r = 0.34$ for Douglas-fir; $r = -0.50$ and $r = 0.52$ for lodgepole pine). Site index in western larch had very
weak correlations with both late season temperatures and VPD ($r = 0.21$ and $r = 0.19$, respectively).

### 4.1.4 Growing Season Radiation

Sites where ponderosa pine and lodgepole pine trees were selected experienced the greatest average amounts of growing season radiation (344783.9 MJ m$^{-2}$ and 337607.5 MJ m$^{-2}$, respectively) with western larch sites experiencing the least (318088.6 MJ m$^{-2}$). Douglas-fir sites averaged 319954.4 MJ m$^{-2}$ and spanned the greatest range of growing season radiation (126088-384701 MJ m$^{-2}$). Growing season radiation is aspect and slope dependent (Fig. 4.16) and is able to pick up some of the variation in topography. Southern aspects receive the greatest amount of growing season radiation and peak in magnitude on 45% slopes. Northern, eastern, and western aspects exhibit declines in growing season radiation as slope increases due to the diffusing of direct beam irradiance.

Relationships between site index and growing season radiation (Fig. 4.17) were weak in all species’ samples. The correlation was negative for ponderosa pine ($r = -0.19$), lodgepole pine ($r = -0.26$), and western larch ($r = -0.33$). Douglas-fir was the only species with a positive (albeit negligible) correlation between these variables ($r = 0.09$). The same trees as in previous figures are highlighted in Fig. 4.21 to emphasize that GSR varied at finer spatial resolutions.
Figure 4.16 Growing season radiation and slope conditioned by aspect.
Figure 4.17 SI and growing season radiation. Shown in red are the same trees highlighted in Fig. 4.2.


4.2 Modeling Results

To determine whether a logarithmic transformation of SI was required in model fitting, Furnival’s Index was calculated for both log-transformed and untransformed SEA₁₁ model (Table 4.4). For all species’ models, modeling SI on the original scale produced the smallest model error as represented as Furnival’s Index. It was concluded from this that a logarithmic transformation was not useful. As a result, only models for SI on the original scale of meters are presented in the subsequent model analyses.

Table 4.4 Furnival’s Index values for model SEA₁₁ using untransformed and log transformed SI response.

<table>
<thead>
<tr>
<th>Species</th>
<th>Furnival's Index (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Untransformed</td>
</tr>
<tr>
<td>Ponderosa pine</td>
<td>3.5</td>
</tr>
<tr>
<td>Douglas-fir</td>
<td>3.3</td>
</tr>
<tr>
<td>Lodgepole pine</td>
<td>2.7</td>
</tr>
<tr>
<td>Western larch</td>
<td>1.8</td>
</tr>
</tbody>
</table>

4.2.1 Geocentric Models

Adjusted R² and RMSE values for each geocentric model and species are in Table 4.5. Response vs. variable scatterplots, quantile-quantile normality plots, and residual plots indicated that the requisite conditions regarding linearity, normality, and homoscedasticity were met for all models. The model form that explained the greatest proportion of variation in SI differed by species. SEA₁₁(LatLon) was the best geocentric model for explaining the variation in SI for all species (Table 4.5). Across species comparisons showed ponderosa pine had the most variation explained by all of the 3 models and western larch had the lowest RMSE. ANOVA F-tests indicated that a better model fit to the SI data could be achieved by adding latitude, longitude and
TPI300 to species specific models containing the SEA_{11} predictors. Ponderosa pine and Douglas-fir models indicated that longitude was a significant predictor (p<0.001) in the geocentric models but was not for lodepole pine and western larch models. TPI300 was significant in ponderosa and lodepole pine models (p<0.001) but was not for Douglas-fir and western larch (p=0.07 and p= 0.27, respectively). The sign of the TPI300 coefficient for all models was negative indicating that site trees in lower spatial positions relative to the neighboring 300 m area were more productive.

**Table 4.5** Adjusted R² and RMSE (m) for all models and species.

<table>
<thead>
<tr>
<th>Model</th>
<th>PP</th>
<th>DF</th>
<th>LP</th>
<th>WL</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Geocentric</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lat/Lon</td>
<td>0.3752 (3.9)</td>
<td>0.2236 (3.1)</td>
<td>0.0938 (3.0)</td>
<td>0.0321 (2.7)</td>
</tr>
<tr>
<td>SEA\textsubscript{11}</td>
<td>0.4772 (3.5)</td>
<td>0.1528 (3.3)</td>
<td>0.2019 (2.7)</td>
<td>0.5507 (1.8)</td>
</tr>
<tr>
<td>SEA\textsubscript{11} LatLon</td>
<td>0.6412 (2.9)</td>
<td>0.3717 (2.8)</td>
<td>0.4535 (2.3)</td>
<td>0.5425 (1.7)</td>
</tr>
<tr>
<td><strong>Biophysical</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>AET/DEF</td>
<td>0.3967 (3.9)</td>
<td>0.0874 (3.4)</td>
<td>0.3661 (2.5)</td>
<td>0.1263 (2.5)</td>
</tr>
<tr>
<td>BIOPHY *</td>
<td>0.5816 (3.2)</td>
<td>0.3698 (2.8)</td>
<td>0.4714 (2.3)</td>
<td>0.4126 (2.0)</td>
</tr>
<tr>
<td><strong>Mixed</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BIOTOP**</td>
<td>0.6285 (3.0)</td>
<td>0.2545 (3.0)</td>
<td>0.4905 (2.4)</td>
<td>0.5548 (1.7)</td>
</tr>
</tbody>
</table>

*Model [21] in section 4.2.2
**Model [15] in section 3.2.2

Predictive surfaces of the SEA\textsubscript{11} (LatLon) model are displayed in Fig. 4.18. These polar plots show the predicted interactions of elevation and aspect for all 4 species with latitude and longitude fixed at 47˚N and -114˚E (Missoula, MT) and slope fixed at 15%. Ponderosa pine and western larch plots both indicate that SI is highest on northeast aspects at low elevations, decreases towards mid elevations and then increases at the upper ranges of elevation. Douglas-fir predicted SI is also highest at the lower elevations on northeast aspects. Increases in elevation
result in a decrease in predicted SI values but at the upper limits of the elevation range the most productive aspect reverses from northeast to south. Lodgepole pine exhibits uniform SI predictions across aspects and for elevations ranging from 1250 m to 1750 m. SI predictions then decrease as elevation increases above 1750 m. Additionally, SI predictions from each geocentric model varied substantially (Table 4.6). SEA_{11} necessarily predicted similar values regardless of geographic location given similar topography. LatLon and SEA_{11}LatLon were able to account for geographic location and, as a result, predictions of SI accounted for the influence of the longitudinal climatic (precipitation) gradient that is present in Montana. Patterns were not detected when plotting each geocentric model residuals against climate variables.

**Table 4.6.** Model predictions for ponderosa pine SI (m) for Missoula and Billings, MT. Slope and elevation are held constant at 0%, and 1000 m, respectively.

<table>
<thead>
<tr>
<th></th>
<th>LatLon</th>
<th>SEA_{11}</th>
<th>SEA_{11}LatLon</th>
</tr>
</thead>
<tbody>
<tr>
<td>Missoula</td>
<td>19.3</td>
<td>19.4</td>
<td>18.9</td>
</tr>
<tr>
<td>Billings</td>
<td>11.9</td>
<td>19.4</td>
<td>12.9</td>
</tr>
</tbody>
</table>
Figure 4.18  Polar plots of predicted SI values using SEA_{Lat/Lon} for each species. Up is north, down is south; location is Missoula; slope is 15%.
4.2.2 Biophysical Models

The adjusted R² and RMSE values from Table 4.5 indicate that the AETDEF biophysical model did not perform as well as the SEA_{11} geocentric models. AETDEF was able to explain more of the variation than the LatLon model for ponderosa pine, lodgepole pine, and western larch. When the interaction of AET and DEF were added to the SEA_{11} model, the variance explained increased for all species and an (ANOVA) F-test indicated that the additions were significant (p<0.001) and better fit the data than SEA_{11} alone. BIOTOP was the best model for lodgepole pine and western larch, explaining approximately half of the variation in site index for each species.

Exploratory nonparametric models based on random forests indicated that January VPD and minimum temperature were the most important variables for predicting SI. A random forests model containing January VPD, January minimum temperature, DEF, AET, and growing season radiation (GSR) had a coefficient of determination of 0.83 for ponderosa pine, 0.74 for lodgepole pine and Douglas-fir, and 0.65 for western larch. When these same explanatory variables were used in a generalized additive model, the partial response curves indicated that the relationships with SI followed broadly linear trends even though the smoothed response curves were extremely variable. Thus, a linear model using these explanatory variables was created for each species having the form:

\[
SI = AET + DEF + VPD_{Jan} + Tmin_{Jan} + GSR + \epsilon
\]  

[20]

The variation explained by these models was compared to the results from generalized additive modeling (Table 4.7).

Not surprisingly, the highly flexible generalized additive model forms resulted in higher R² values and lower RMSE values. More importantly, although these explanatory variables were
selected as the best predictors based on the random forests algorithm, their ecological relevance is dubious: winter temperatures and VPDs do not directly impact tree height growth except possibly through damage to apical buds.

**Table 4.7** Adjusted $R^2$ and RMSE (m) from additive and linear models using AET, DEF, VPD$_{Jan}$, Tmin$_{Jan}$, and GSR [20] to estimate site index.

<table>
<thead>
<tr>
<th>Species</th>
<th>Model Adjusted $R^2$ (RMSE)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>GAM</td>
</tr>
<tr>
<td>Ponderosa Pine</td>
<td>0.7580 (2.3)</td>
</tr>
<tr>
<td>Douglas-fir</td>
<td>0.5780 (2.2)</td>
</tr>
<tr>
<td>Lodgepole Pine</td>
<td>0.7210 (1.5)</td>
</tr>
<tr>
<td>Western Larch</td>
<td>0.7700 (1.2)</td>
</tr>
</tbody>
</table>

To build a more ecological rational model AET, DEF, growing season mean monthly maximum temperature (MTMAX), aggregated growing season monthly VPD’s (GSVPD) and growing season radiation (GSR) relationships with SI were also explored using a generalized additive modeling approach. Partial response curves (e.g., Fig. 4.19) and ANOVA F-tests ($p<0.001$) indicated that the predictors GSVPD and MTMAX should be described parametrically using quadratic terms, but that the effects of other variables were best approximated by linear terms. That is, mean SI was described as:

$$
SI = b_0 + b_1AET + b_2GSVPD + b_3GSVPD^2 + b_4MTMAX + b_5MTMAX^2 + b_6GSR + b_7DEF + \varepsilon
$$

[21]

Fit statistics for the generalized additive model and linear model are listed in Table 4.8 and coefficients for [21] are presented in Table 4.9. The joint effect of MTMAX and GSVPD are shown in Fig 4.21 and joint effects of DEF and GSVPD are shown in Fig. 4.22.
Figure 4.19  Partial response curves of Douglas-fir site index to GSVPD and Deficit from fitting a GAM with smoothing spline effects for GSVPD, MTMAX, AET, DEF, and etc.

Table 4.8 Adjusted R² and RMSE (m) from additive model using AET, DEF, GSVPD, GSTMAX and GSR and linear model with quadratic terms [21] model to estimate site index.

<table>
<thead>
<tr>
<th>Species</th>
<th>GAM</th>
<th>Linear</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ponderosa Pine</td>
<td>0.7840 (2.1)</td>
<td>0.5816 (3.2)</td>
</tr>
<tr>
<td>Douglas-fir</td>
<td>0.5530 (2.3)</td>
<td>0.3698 (2.8)</td>
</tr>
<tr>
<td>Lodgepole Pine</td>
<td>0.7120 (1.5)</td>
<td>0.4714 (2.2)</td>
</tr>
<tr>
<td>Western Larch</td>
<td>0.7890 (1.1)</td>
<td>0.4126 (2.0)</td>
</tr>
</tbody>
</table>

Table 4.9 Biophysical linear model [21] coefficients.

<table>
<thead>
<tr>
<th>Species</th>
<th>AET</th>
<th>DEF</th>
<th>GSR</th>
<th>GSVPD</th>
<th>GSVDP²</th>
<th>MTMAX</th>
<th>MTMAX²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ponderosa Pine</td>
<td>0.155</td>
<td>-0.098</td>
<td>-1.063E-04</td>
<td>94.978</td>
<td>-3.789</td>
<td>-68.541</td>
<td>3.517</td>
</tr>
<tr>
<td>Douglas-fir</td>
<td>0.075</td>
<td>-0.064</td>
<td>2.359E-05</td>
<td>39.099</td>
<td>-1.627</td>
<td>-14.615</td>
<td>0.985</td>
</tr>
<tr>
<td>Lodgepole Pine</td>
<td>0.049</td>
<td>-0.012</td>
<td>-6.228E-05</td>
<td>26.845</td>
<td>-1.364</td>
<td>0.912</td>
<td>0.022</td>
</tr>
<tr>
<td>Western Larch</td>
<td>0.055</td>
<td>0.053</td>
<td>-7.599E-05</td>
<td>-70.092</td>
<td>3.090</td>
<td>39.869</td>
<td>-2.303</td>
</tr>
</tbody>
</table>
As expected, generalized additive models explained the greatest amount of variation in SI for all species and were able to show possible interactions among biophysical variables. Fig. 4.20 provides a visualization of one possible interaction between DEF and GSR. It indicates that sites with low DEF (more available water) and low GSR and sites with low deficit and moderate GSR are the most productive. While these semi-parametric models outperformed all of the other models, they were not utilized as result of the difficulty in parametrically describing splined terms. Generalized linear models were considered with both the log and square root link but there was little difference in the model fit except for western larch (R² = 0.47 and R² = 0.49, respectively). The biophysical model (21) outperformed the SEA₁₁, AETDEF, and LatLon models for all species except for western larch where SEA₁₁ model accounted for a greater share of the variation. The variation explained by the biophysical models was similar to the SEA₁₁(Lat/Lon) and SEA₁₁ (AETDEF) models for each species, indicating that the biophysically based predictors account for a large portion of the variability previously captured by the terrain metrics (TPI, elevation, aspect, slope) and geographic location (latitude, longitude). Table 4.7 provides adjusted R² and RMSE for all geocentric and biophysical linear models.

**Figure 4.20** Estimated joint effects of deficit and growing season radiation from Douglas-fir GAM on SI. Contours are SI in meters.
Figure 4.21 Estimated joint effects of mean growing season maximum temperature and aggregated growing season VPD on SI. Contours are of SI in meters.
Figure 4.22 Estimated joint effects of mean growing season maximum temperature and annual deficit on SI. Contours are of SI in meters.
Chapter 5

Discussion

5.1 Data Limitations

Forest productivity varies across landscapes as a function of regional climate, the transformations of climate induced by local physiography, and the interaction of those forces with the underlying soils. In addition, within relatively homogeneous tracts of forest land, individual tree productivity varies as a function of microsite conditions (i.e. microclimate and fine scale topography), genetics, topographic position, and even mycorrhizal associations. The low adjusted R² values (< 0.65; Table 4.5) obtained by the site index models evaluated in this study can be attributed in part to the fine scale variability in the estimates of SI. This variability is a direct result of using tree-level SI values rather than, for example, stand-level averages. Monserud (1984) provides results from a study using different sample sizes to calculate site index for an individual stand. The results from the study indicated that using a sample size of only one site tree produced SI biases of up to 4.9 m when compared to averaging multiple site trees (15-20 trees). Thus, using individual tree SI is a known source of error however, it is impossible to determine the magnitude of the actual error since no stand information was provided in the dataset. Determining a stand level SI using multiple site trees is common practice in forestry. Foresters are interested in stand SI which is defined as the averaged height of the dominant and codominant size classes in a stand at age 50. Tree level SI misses a large component of the stand productivity by not taking into account the height of other dominant and
The variation in tree level SI is also problematic when describing the relationships between SI and topography or climate. Figure 4.4 shows that trees on sites of the same aspect and elevation (within one climate pixel) can have differences in SI estimates of up to 7.9 m. Conversely, within such pixels, the same values of climate variables are given to multiple SI trees that differ in aspect, elevation and slope, which disregards the effects that complex topography has on microclimate. Chen et al. (1999) provided evidence that at the tree level, growth is generally influenced more by microclimate (e.g. 5 m × 5 m resolution) than it is by processes operating at 800 m × 800 m scales; thus without fine scale climate information, fine scale variation in tree productivity cannot be fully explained.

Another potential source of variation in the present study is that productivity was inferred using regional SI equations developed by Milner (1992). Besides the potential for error in the specification of the equations themselves, the estimates are also subject to height and age measurement errors. The equations are used to either predict how tall a tree will be (or was) at breast height age 50. However, these equations are unable to provide accurate SI estimates if height and age are measured with error when estimating SI using height-age based equations. When using regional SI equations, measurement errors can exacerbate SI when estimates or predictions are needed for younger or older trees. From Fig. 4.2, a strong negative relationship is
evident between SI and breast height age. In principle, no such relationship should exist, since the equations should be equally capable of proactively and retroactively estimating height at the reference age on all sites. There are two plausible reasons for this: 1) older trees were not available for selection on more productive sites (because these sites were previously harvested), or 2) the SI equations do not properly account for reduced height increment at advanced ages, leading to low estimates of height at the reference age. A solution to this problem would be to directly measure SI using stem analysis techniques (Monserud 1984b). By sectioning the stem at various heights and counting growth rings, this method can provide the actual height at breast height age 50 (for trees of at least that age) and is thus the most accurate method for evaluating SI. Previous studies relating SI to climate (Monserud et al 2006, McLeod and Running 1987, Curt et al. 2001) have performed stem analysis on multiple site trees to estimate SI. In order to develop precise models of SI from climatic and/or topographic variables analogous methods should be considered in future studies.

Another issue with using SI equations is that they are based on relationships observed over broad spatial scales. Milner’s (1992) equations do not distinguish between dominant height growth trajectories of various habitat types or genetic populations. Yet habitat type and genetic populations within tree species (especially Douglas-fir) have been shown to explain a fifth and half of the variation of SI, respectively (Monserud 1984b; Monserud and Rehfeldt 1990). Habitat type and genetic information was not collected in this study and it is likely that habitat types and genetic populations were not equally represented in the sample. Monserud and Rehfeldt (1990) indicated that Douglas-fir genotypic variation was strongly correlated with environmental gradients (mainly elevation gradients; r = 0.76) and overall moderately correlated with SI (R²=0.42). The study concluded that the frequency and duration of frost free periods,
occurring along elevation gradients, acts as a genetic pressure that stratifies Douglas-fir into distinct genetic populations. The growth responses of these populations in turn respond differently to various climate factors and can result in different productive capacities (and possibly unique dominant height growth trajectories).

It is also important to note that 89 sites were located on private timberland held by the Plum Creek Company (Zuuring and Milner 2008). Timber companies often utilized improved genetic stock to increase timber yields. While it is unknown from this dataset, the sampled trees could have been subject to genetic improvement, or fertilizations, or site preparations. One of the assumptions underlying the application of SI as a measure of productivity is that it is constant over time however, these types of improvements allow the productive potential to be altered.

Beyond SI, another important source of error relevant to the identification and calibration of productivity models has to do with the interpolated climate variables. Meterological data, for the most part, are unavailable throughout the landscape except where physical observations are taken. Without such observations, estimates are made by interpolating meteorological data between stations with a model such as PRISM (Daly et al. 2008). Thus, the PRISM climate variables used for this study are not without error. This is important because it is well established that in a regression modeling context, errors in predictors not only render the identification of trends more challenging, they also lead to biased estimates of those predictors’ effects.

Soil information obtained from STATSGO (Soil Survey Staff 1995) is another source of error. This data product was created to inform the management and planning of broad general areas – at resolutions appropriate for multicounty, state and multistate regions –was modeled at a 1 km x 1km resolution. Soil depth, texture, water holding capacity and many other properties can
vary at small scales (Sharma and Luxmoore 1979) and their effects cannot be adequately accounted for using the STATSGO product. Moreover, using coarse soil information to inform PET equations for climatic water balance has ramifications for the accuracy of AET and DEF estimates. This includes the oversimplification of the effect of water stress (Fig. 3.1) on AET and that climatic water balance models utilize only water holding capacity and do not account for other physical properties of the soil that can influence AET.

Many studies have shown that soil properties are important predictors of SI (Carmean 1975; Klinka and Carter 1990; Curt et al. 2001; Corona et al. 2000). However, conclusions vary as to which properties are of the greatest importance. Among the properties used in past studies you will find calcium carbon content, pH, texture, water holding capacity, soil particle size, and mineralizable nitrogen. While these contribute to overall tree and stand productivity, there is no agreement as to which are of the greatest importance. In addition, in a large scale study Monserud et al. (1990) found that after evaluating the soil nutrient status and water holding capacity at multiple plots they were unable to provide any meaningful relationships between measured soil properties and SI. Their negative findings indicate the complexity of soil-tree relationships and the challenges of describing exactly how soil contributes to productivity.

Lastly, the errors in the many individual estimates of temperature, VPD, and precipitation are cascaded into the estimates of the integrated terms PET, AET, and DEF. Fine resolution estimates created with models and then combined with other fine resolution models to create a final product does not necessarily result in estimates that are accurate at fine resolutions. While it is beyond the scope of this study, error propagation from climatic variables to water balance metrics should be considered in future evaluations of the relationships between climate and forest productivity.
5.2 Distribution of Trees

The quantity, quality, and distribution of the data ultimately dictate the strength and scope of predictive models. This study utilized 877 SI trees, distributed throughout Montana, to examine the relationships between SI, topography, and climate. While this study differs in the method for estimating forest SI, it does have more observations of SI taken over a broader range of climatic and topographic conditions than previous studies (McCleod and Running 1987; Curt et al. 2001; Klinka and Carter 1990; Monserud 1990).

In most cases trees were selected across the multidimensional ranges of slope, elevation and aspect (Table 4.3). Elevation was the only topographic variable that revealed a substantial relationship with SI and this was species dependent (Fig. 4.5). Ponderosa pine SI responded positively to elevation and the other species showed weak but negative relationships.

Ecologically, ponderosa pine is a lower elevation species where the duration of the growing season is long and, in general, the evaporative demand is much higher. Increases in elevation coincide with cooler temperatures and, as a result, less evaporative demand. Such a decrease in water stress may be why ponderosa pine SI responded positively to increases in elevation.

Douglas-fir SI trees were observed across the broadest range of elevations (Fig. 4.5, Table 4.3). Lodgepole pine, ponderosa pine, and western larch exist at lower elevations than are observed in this study, but it is possible that at those elevations other species dominate the forest canopy and are more suitable for SI evaluations.

The climate space spanned by the selected trees was surprisingly constrained. For example, temperature and VPD were highly correlated (Fig. 4.12). SI trees were never selected in areas where high temperatures coincided with low VPD nor where low temperatures and high VPD occurred. While this makes estimation difficult for conditions where high temperature and
low VPD occur it is important to remember that, aside from in the tropics, these conditions require a simultaneous abundance of water and energy. So even though the data come from a limited portion of the temperature × VPD space, this should not affect the applicability of the BIOPHYS model if used within the Interior Northwest region. The high correlation will affect interpretation because the effect of VPD is carried by temperature and the effect of temperature is carried by VPD. As a result, when both VPD and temperatures are in the model the individual effects will be estimated with poor precision. This can be remedied by either collecting additional data to fill incomplete variable spaces (e.g. high temperatures with low VPD) or by searching for the underlying causes that may explain the interrelationships of the predictors (Chatterjee et al. 2000). This study calculated VPD using Tmax, invariably linking the two variables together so that increases in Tmax result in increases in VPD. A possible solution would be to calculate VPD using relative humidity or by physically measuring or interpolating VPD across the landscape.

As expected, mean maximum temperatures and VPD decreased with elevation for all species (Fig. 4.13) and the former had an average lapse rate of 5.7 °C for every 1000 m. As a result of this relationship, coverage over a wide range of elevations, temperatures, and VPD was constrained. High VPD and temperatures were not observed at higher elevations and low VPD and temperatures were not observed at lower elevations. No constrained relationship existed for slope and aspect.

AET-DEF relationships are different for each species (Fig. 4.9). Ponderosa pine and Douglas-fir exhibited a strong negative relationship between AET and DEF, while western larch and lodgepole pine sites exhibited a positive relationship. While complete coverage is desirable, biogeographical theory indicates that certain species, as well as ecosystems, will occupy these
AET and DEF climate niches (Stephenson 1990; Lutz et al. 2010). The fact is that certain climatic water balance profiles may be more conducive to one ecosystem or species over another. For example, locations with high DEF and low AET may favor a species that is more adapted for high heat stress and little biologically available water. From these data, it is apparent that western larch may not thrive in a competitive environment under low AET and high DEF conditions where Douglas-fir and ponderosa exist (Fig. 4.9). The SI trees were selected from multiple climate zones throughout Montana based on precipitation, but this is not to say that all conditions of AET and DEF are represented and observed relationships could be an artifact of the sampling methodology.

Species specific AET responses to temperatures and VPD indicated an inverse relationship with ponderosa pine and weak relationships with the other species (Fig. 4.10). Douglas-fir, lodepole pine, and western larch had coverage over both climate variables and ponderosa pine lacked AET observations at low monthly maximum temperatures. DEF and monthly maximum temperatures showed a strong positive relationship for all species (Fig. 4.11). All species lacked moderate to high DEF values at low monthly maximum temperatures.

Overall, this large data set was able to cover much of the topographic and climatic ranges that are characteristic of the forested Montana landscape. While total coverage is desirable it also may be impossible unless the search for site trees is broadened beyond western Montana. Specifically, ponderosa pine and even more so Douglas-fir have wide geographic ranges that extend from Mexico to the U.S. southwest states, and include California, Oregon, Washington, and British Columbia. A dataset with an equally large scope would be better able to capture all combinations of temperature, VPD, AET, and DEF levels and provide a much stronger basis for understanding the effects of these variables on SI.
Additionally, the four species in this study tend to be dominant in specific environmental niches. Ponderosa pine trees tend to be most productive and dominate at lower elevation sites. As elevation and subsequent moisture increase it becomes outcompeted by Douglas-fir as the new climax species (Arno 1980). Lodgepole pine has adapted to survive a wide range of climate conditions including the ability to survive extreme winter temperatures at higher elevations. Seedlings are capable of withstanding frost injury where other trees would incur damage and as a result of this adaptation, lodgepole pine has the ability to dominate under conditions inherent at higher elevations (Baker and Langdon 1990). Western larch is a species that requires a moist environment with low temperatures limiting its upper elevation range and deficient moisture limiting its lower elevation range. It is most productive at mid elevations where combinations of aspect and elevation provide conditions where water stress is low (Baker and Langdon 1990). Douglas-fir, by contrast, has the ability (and possible the genetic variability) to grow in a suite of climate and topographic conditions (Weiskittel et al. 2012). These species have evolved to exist and persist within a specific range of climate given a specific spatial scale and it is highly likely that the entire environmental spectrum of each species was not represented in this study. While this is not a limitation of this study given current climatic conditions and regional scale, it will be difficult to estimate SI under novel climatic conditions that were not represented in this study. If the sampled climatic ranges of these species were broadened then the models presented may not have to be extrapolated beyond the measured climatic conditions presented in this study in order to consider future climatic conditions.
5.3 Performance of Site Index Models

In the beginning of this study, it was hypothesized that the more biologically meaningful variables (i.e. AET and DEF) would explain the greatest amount of variation in SI. The results indicate that SI is correlated with these variables (Figs. 4.14-4.15) but the biophysical models advanced do not attain $R^2$ values appreciably higher than the geocentric models (Table 4.5). There are several possible reasons for this including: i) SI and topographic variables were obtained at high spatial resolutions (individual tree; 30 m × 30 m) while climate and climatic water balance variables were obtained at coarse resolutions (800 m × 800 m); ii) correlations between individual terrain variables and SI tends to be stronger than those between SI and climatic water balance; and iii) a large amount of uncertainty in the individual values of the predictor variables exists and affects the ability to discern relationships with SI.

Looking across models, it was most surprising that latitude and longitude alone were able to explain as much as 20-30% of the variation in SI for some species (Table 4.5). These models show that western sites are more productive, likely as a result of the decline in annual precipitation as you move east through Montana as well as of the orographic effects caused by the predominantly north-south mountain ranges in western part of the state. This finding is consistent with the findings of Monserud et al. (1990) who found longitude to be a significant contributor to SI predictions.

The varying strengths of the relationships between longitude and SI result from the differential species distributions over multiple climate zones that influence water availability (Littell et al. 2008). Ponderosa pine has the maximum range of longitude in this data set (and in the state of Montana more generally) and therefore is able to best reflect the relationship between productivity and the east-west precipitation gradient. Douglas-fir has the second largest
geographic spread in this sample and results in the next best fitting LatLon model. Interestingly, despite the species’ extensive geographic distribution in Montana, longitude did not appear to be associated with lodgepole pine SI. This could be an artifact of a geographically-truncated sample distribution (few trees from east of the Continental Divide; Fig. 4.1) or may result from the higher altitude profile of this sample (Fig. 4.3), with high-elevation climatic effects dampening those of geographic position. Geographic variation in western larch SI was essentially nonexistent, most likely as a result of this sample being distributed only in northwestern Montana (Fig. 4.1).

Yet while some variation in SI is explained by longitude (and latitude), the relationship is neither biologically relevant nor useful in terms of understanding productivity in an era of anticipated climate change. The productivity today at a given latitude and longitude (and at that position’s implicit elevation, aspect, etc.) is not expected to remain constant under different future climate scenarios. Thus predictive models of forest productivity should move away from using geographic locations as predictors and toward the use of variables that directly influence productivity and that respond to changing climate.

Topography has long been associated with forest structure, species distribution, and productivity (Lookingbill and Urban 2005). The effects of topography do not act singularly but are a result of the intertwining combinations of elevation, aspect and slope (Stage and Salas 2007). Of all the species in this study western larch and ponderosa pine had the greatest variance explained using the complex combination of topographic predictors in the SEA11 model (Table 4.5). This was in part a result of the two species spatial distributions (Fig. 4.3). Productive ponderosa pine SI trees tend to occupy middle to lower elevation sites on southern and western aspects while productive western larch SI trees tend to inhabit middle to lower elevation northern
aspects. These relationships, which are absent in the lodgepole pine and Douglas-fir distributions are a probable reason why the SEA$_{11}$ model was able to explain the most variation in site index for both species.

Douglas-fir and lodgepole pine SI had similar response to elevation, aspect and slope but overall the bivariate correlations were low. Douglas-fir SI trees varied more at any given level of elevation, slope, and aspect had the largest variance among all other species. Statistically, this indicated that sites throughout the topographic variable spectrum were not appreciably different in terms of productivity. This finding comes in spite of the fact that Douglas-fir site trees were found under a wide range of topographic conditions, and suggests that sites of equivalent productivity can be found at very different topographic positions, perhaps as a result of varying macroclimate.

Localizing the effects of topography using the SEA$_{11}$ (LatLon) model dramatically increased the variance explained and reduced RMSE for all species, and resulted in the best fitting models for ponderosa pine and Douglas-fir (Table 4.5). The improvement is a result of adding another spatial dimension to slope, elevation and aspect, effectively accounting for the differences in SI values topographically and along the precipitation gradient previously discussed. Comparing SI predictions (Table 4.6) from this model using geographic positions of 47°N and 114°W (Missoula, MT; elevation 1450 m) and of 46°N and 109°W (Billings, MT; elevation 953 m) differences of up to 6.9 m in SI. Moving from west to east, ponderosa pine SI is expected to decline by 6.1 m, Douglas-fir and lodgepole pine SI by 3.0 m, and western larch SI by 1.5 m given the same topographic profile. For the two species with the greatest distribution along the longitudinal (precipitation) gradient, ponderosa pine and Douglas-fir, this model
performs the best of all model forms considered. In addition, as seen in Fig. 4.18 the model allowed the optimal aspects for productivity to vary with elevation.

Yet again, ecologically, the mechanism creating favorable conditions for tree productivity is not variation in topography but rather the manner in which topography influences climate. Figure 4.13 shows that temperatures and VPD decrease with elevation and result in higher or lower productivity depending upon the species. Aspect conditions the duration and timing of solar energy. In the northern hemisphere, north and east aspects receive solar radiation during the morning when temperatures are cooler. This creates an environment where moisture stress and evaporative demand is low. This low demand also allows snow to persist on north and east aspects and results in a mediating effect on temperature and water stress. Alternatively, south and west aspects receive the majority of solar radiation during the afternoon when temperatures are much warmer. This can create a large atmospheric demand for water that can limit the growth of trees by increasing water stress, especially at lower elevations where temperatures are warmer and the growing season is longer (Dyer 2009).

Unfortunately, when predictions are needed for forest productivity under alternative climate scenarios, the same deficiencies associated with predicting site productivity from latitude and longitude are also associated with predictions based on topography. Topography, barring a cataclysmal event, will remain static as macroclimate changes. Ultimately, the only solution for predicting SI in a manner that will function under future climate regimes is to build empirical models using climatic variables and plant relevant metrics such as AET and DEF.

The results of this study indicated that a simple climatic water balance model was unable to explain a substantial proportion of the variation in SI for any species (Table 4.5). The greatest variation explained by AET and DEF alone was for ponderosa pine (adjusted \( R^2 = 0.3967 \)) and
lodgepole pine (adjusted $R^2 = 0.3661$); the models for Douglas-fir and western larch had very low adjusted $R^2 (< 0.13)$. This low explanatory power may be a result of calculating climate variables at an 800 m x 800 m resolution. In doing so, climate is essentially averaged for an area where SI and microclimatic factors can vary dramatically. Briggs and Wickramasinghe (1990) were able to explain 60% of the variation in forest volume growth with plot-level estimates of AET and Littell and others (2008) showed that DEF (water limitation) of the previous year was highly correlated with productivity measured as tree ring growth. Overall, these results indicate that the mismatch in resolutions needs to be remedied in order to capture more of the variability in SI using these variables, either by producing finer resolution climatic water balance products or by estimating SI at the stand level.

Perhaps the most common and successful method for predicting SI is the use of a combination of climatic water balance, climate and physiographic variables (Klinka and Carter 1990). In this study, such combinations were considered in two distinct models. The first model used AET, DEF, GSVPD, MTMAX, and GSR (BIOPHY) and the second added climatic water balance variables (AET and DEF) to SEA$_{11}$ (BIOTOP). These two models are referred to as BIOPHY and BIOTOP below.

BIOPHY was able to explain almost half of the variation in SI for each species and doubled the amount of variation explained by the topographic model (SEA$_{11}$) for Douglas-fir and lodgepole (Table 4.5). The model coefficients (Table 4.9) indicated that all species SI respond positively to AET and all but western larch respond negatively to DEF. Coefficients also indicated that simultaneous increases in MTMAX, GSVPD, and DEF will increase expected SI values for all species up to a species specific threshold (Fig 4.21 and Fig 4.22). At this point, expected SI will subsequently decline with increasing MTMAX, GSVPD and DEF. Ponderosa
and lodgepole pine SI respond negatively to GSR and western larch and Douglas-fir SI respond positively.

These responses appear to be reasonable when the habitats, ecology, and physiology of each species are considered. AET is the integration of biologically available water and energy that trees use to grow and therefore as AET increases there is more potential for productivity. DEF is a measure of dryness and indicates how much more evapotranspiration could have occurred if the demands of the atmosphere could have been met by additional water. The greater this value the more water stress occurs and decreases in productivity are realized. Western larch typically grows in mesic sites where water is often not limiting and the relationship between DEF and SI is ambiguous for this species (Fig. 4.15). The combined effects of high GSVPD, MTMAX, and GSR are extreme at lower elevations where ponderosa pine is found. Together these three variables create conditions where available energy is high and water availability is low as a result of the high evaporative demand. Lodgepole pine and western larch trees are generally found at higher elevations and north aspects, respectively (Fig. 4.3), where energy is limiting. For this reason, as GSVPD and MTMAX increase, the energy of the site increases and creates conditions that can facilitate greater productivity.

The variation explained by the biophysical models, while low, are consistent with findings of other studies. Corona et al. (1998) were able to explain 57% of the variation in Douglas-fir plantation site index using aspect, water balance surplus, clay content, calcium carbonate content, and annual rainfall. Curt et al. (2001) explained 40% of the variation in Douglas-fir SI using soil nutrient status, elevation, water seepage index, and topographic index. These studies still used static variables that may not differ under climate change scenarios making predictions of productivity under novel climate scenarios difficult to assess.
The most practical approach to estimate SI under different climate scenarios is to build models using only climate variables. Monserud et al. (2006) used the climate variables growing degree days, Julian date when growing degree days equals 100, and July mean temperature. Their model only explained 27% of the variation in lodgepole pine SI. A process modeling approach used 3PG and DAYMET climate estimates explained 55% of the variation in Douglas-fir SI but still had an RMSE of 9.1 m (Swenson et al. 2005) Results from the present study are similar but RMSE values are much lower (<3.2 m for BIOPHY; Table 4.5).

Other studies using climatic information to estimate SI produced better results include those by Klinka and Carter (1990) and Weiskittel et al. (2011b). The latter study may have an overly optimistic coefficient of variation from using the Random Forest method for analysis. The present study used the same method and was able to explain 81% of the variation in SI, but using climate variables with little direct relevance to tree growth or productivity, suggesting that Random Forest may not be the most appropriate statistical tool when a large number of intercorrelated predictor variables are available for analysis.

Klinka and Carter (1990) were able to explain 72% of the variation in SI using growing season AET, growing season DEF, and mineralizable nitrogen. While the present study is similar aside from using nitrogen, Klinka and Carter used a water balance model specified by Spittlehouse and Black (1981) that accounts for the influences of the current vegetation on evapotranspiration (i.e. interception) and observed soil depth and texture. In addition, their water balance model uses the Priestly-Taylor method for calculating the evaporative demand of the atmosphere instead of the Penman-Monteith method used here (see Section 3.1.3). Fisher et al. (2005) provided results that indicated that the Priestly-Taylor method has the capacity to produce accurate estimates, superior to Penman-Monteith, of PET when compared to eddy covariance.
tower measurements. Future studies of the relationships between SI and climatic water balance should consider using these methods as they offer improvements over a coarse soil model and potentially a more accurate method of estimating PET. Of course, the ability to do so hinges on the availability of accurate soil information across landscapes.

Adding AET and DEF to a model using the SEA$_{11}$ predictors increased the variance explained for all species and was the best fitting models for lodgepole pine and western larch SI (adjusted $R^2 = 0.4905$ and 0.5548, respectively; Table 4.5). While improvements were seen over the SEA$_{11}$ model, the effect was similar to the addition of latitude and longitude suggesting that coarse resolution AET and DEF were able to pick up some of the same climate gradient information carried indirectly by fine scale geographic coordinates. Still, since AET and DEF were not estimated at the same resolution as topographic or geographic information, a large amount of the variation in SI cannot be explained by these current estimates of climatic water balance. The SI trees selected in this study simply exhibit too much variability within 800 m $\times$ 800 m pixels. The resolution does not reflect our understanding of how tree growth responds to climate but is rather a limitation of technology (fine-scale climate estimates would require large computational resources) and information (accurate soil and precipitation data remain elusive). Across complex topography there are many microclimates favoring productive forest growth but these exist at small spatial scales. Until climate can be accurately modeled at finer spatial resolutions the most practical option for accurately estimating long-term forest productivity may be to measure tree growth directly at the stand level.
Chapter 6

Conclusions

Tree productivity is the expression of the synchronization of multiple interplaying site factors. Broadly speaking, these factors include the energy and water budgets of a site which are in turn influenced by climate and soils. While there is a long tradition in forestry of using topography to describe where the most productive sites occur, predicting future long-term productivity under alternative climate scenarios is impossible when topographic variables are used. Instead, growth models based on climate metrics are the only possible solution. To create the best models, accurate data is a fundamental requirement. Without it, the relationships between long-term productivity, energy and water budgets will be difficult to discern. This study provides evidence that there is a relationship between SI (long-term productivity) and climate but also identifies numerous shortcomings and opportunities for improvement, both in terms of data and analytical methods.

One of the original hypotheses stated that the climatic water balance metrics, AET and DEF, would be able to explain the majority of the variation in site index. After analyzing the data and models, it was apparent that this was overly optimistic. The data and models provide results indicating that a relationship does exist but that it was overwhelmed by fine scale variability in tree SI. Additionally, the fine scale variability obscured relationships with other climate variables. This is likely a major factor in the inability of climate-based models to explain an appreciable amount of the variation in SI.
Previous studies have shown AET and DEF to be associated with productivity. AET reflects the amount of biologically available energy with higher values indicating higher amounts of productivity. DEF is a measure of water stress and is generally negatively associated with plant production. It was originally stated in my hypotheses that AET would be positively correlated with productivity and vice versa for DEF. The findings from the study confirm this to be the case for ponderosa pine, Douglas-fir, and lodgepole pine. However, western larch site index was positively correlated with both AET and DEF. To make a stronger conclusion however, more western larch SI data are required. This is because there are a few data points at the extremes of the climatic water balance space which are heavily influencing this relationship.

I am unable to draw a definitive conclusion regarding whether or not estimates of climate produced by current technology are successful at predicting SI. At one end, the climate pixels were at a resolution too coarse to pick up the fine scale variability in site index. On the other hand, if stand site index was assessed then potentially the estimated climate would be at a more appropriate resolution (800 m × 800 m ≈ 160 acres).

Future studies should consider evaluating stand SI and implementing a stem analysis protocol. This will keep methods consistent with other similar studies and it is the established, standard method in forestry for developing site curves. Currently, climatic information is only available at 800 m × 800 m resolutions, and there is a need to better understand the error levels and error propagation pathways associated with this information and with integrated measures like AET. Using actual climatic data or climate models with proportional resolutions may provide an improved basis for identifying relationships between climate and forest site productivity.
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