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Spatial and temporal reconstruction of twentieth-century growth trends in a naturally-seeded pine forest

Biondi, Franco, Ph.D.

The University of Arizona, 1994
SPATIAL AND TEMPORAL RECONSTRUCTION OF TWENTIETH-CENTURY
GROWTH TRENDS IN A NATURALLY-SEEDED PINE FOREST

by

Franco Biondi

A Dissertation Submitted to the Faculty of the
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For the Degree of
DOCTOR OF PHILOSOPHY
WITH A MAJOR IN WATERSHED MANAGEMENT
In the Graduate College
THE UNIVERSITY OF ARIZONA

1994
As members of the Final Examination Committee, we certify that we have read the dissertation prepared by Franco Biondi entitled SPATIAL AND TEMPORAL RECONSTRUCTION OF TWENTIETH-CENTURY GROWTH TRENDS IN A NATURALLY-SEEDED PINE FOREST and recommend that it be accepted as fulfilling the dissertation requirement for the Degree of Doctor of Philosophy.

Dr. Malcolm K. Hughes

Dr. James O. Klemmedson

Dr. Thomas W. Swetnam

Dr. Lisa J. Graumlich

Dr. Charles W. Stockton

Dr. Donald E. Myers

Final approval and acceptance of this dissertation is contingent upon the candidate's submission of the final copy of the dissertation to the Graduate College.

I hereby certify that I have read this dissertation prepared under my direction and recommend that it be accepted as fulfilling the dissertation requirement.

Dissertation Director

Dr. Malcolm K. Hughes
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[Handwritten signature]
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To my parents, Bianca & Cesare
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ABSTRACT

This research uncovered growth trends from 1920 to 1990 in a stand of southwestern ponderosa pine (Pinus ponderosa Dougl. ex Laws. var. scopulorum), and investigated the role of climate and competition in shaping the observed trends. I focused on a 800x400-m permanent plot maintained by the U.S. Forest Service since 1920 near Flagstaff, Arizona. Temporal growth trends were quantified by size class using a mixed linear model applied to forest inventories, repeated at 10-year intervals. Tree density and stand basal area increased from 1920 to 1990, but growth rates of individual trees declined regardless of size class. Growth of large pines, whose density increased slightly, declined more than that of small pines, whose density almost tripled. I argued that competition for resources reduced growth rates of large trees more than those of small trees.

Geostatistical analyses showed that, from 1920 to 1990, stem size was spatially autocorrelated over distances no greater than 30 m, a measure of average patch diameter. Tree density increased by increasing the number of pine groups rather than their horizontal dimension. Increased tree crowding corresponded to lower average, variance, and spatial dependence of individual growth rates. Since growth variation was less related to inter-tree distance at higher tree densities, density-dependent limitation of tree growth did not necessarily correspond to distance-dependent growth rates.

No significant trend from 1910 to 1990 was found in climatic variables computed
from daily meteorological records. Dendroclimatic analyses showed that climate-tree
growth relations had not significantly changed over the twentieth century. Annual growth
of both large and small pines was positively related to winter snowfall and to July
monsoon rainfall. Periodic basal area increment obtained from dendrochronological data
revealed that forest inventories over-estimated growth rates, especially for small pines.
On the other hand, tree-ring chronologies developed using different standardization
options showed different temporal trends. Repeated forest inventories quantified growth
of individual trees and of the entire stand, but integrated bark and wood increment.
Dendrochronological data had superior temporal resolution and accuracy, but their limited
spatial coverage hindered representation of growth trends for the entire stand.
I. INTRODUCTION

I.1. Preamble

The concentration of greenhouse gases in the atmosphere has increased over the last century (Schlesinger 1991). As a consequence, widespread modification of climatic regimes may occur (Ramanathan 1988, Manabe and Stouffer 1993, Schneider 1994). The threat of rapid global climate change has fueled the need for predicting regional climate with sufficient specificity and reliability to aid national and international policy-making (IPCC 1990, 1992). Understanding and possibly forecasting changes in the Earth's climate system requires focused studies on the physical, geological, chemical, biological and social processes that influence Earth system behavior. In particular, climate change and ecological dynamics are intimately linked at large spatial and temporal scales (Running and Nemani 1991). Assessing sensitivity and responses of terrestrial ecosystems to global change phenomena is crucial to clarify interactions between biogeochemical cycles and the Earth's climate (Schlesinger 1991). For instance, northern temperate and boreal forests play a major role in the sequestration of atmospheric CO$_2$ (Tans et al. 1990, Wofsy et al. 1993, Dixon et al. 1994). Reconstructing past spatial and temporal growth trends in these forest types contributes to the refinement and validation of simulation models used to predict the future state of the Earth's systems.

Woody plants have a dominant role in land-surface vegetation. Longevity of tree
species makes them suitable to study long-term effects of environmental variability on primary productivity. Previous research on forest-climate interactions included gap models of successional dynamics (Botkin et al. 1972, West et al. 1980, Shugart 1984, Kienast and Kräuchi 1991), process-based ecophysiological models of forest ecosystems (Dixon et al. 1990, Bossel et al. 1991, Running and Gower 1991, Pacala et al. 1993), mixtures of the previous two model types (Friend et al. 1993), and dendrochronological reconstructions of primary productivity (Graumlich et al. 1989), of climatic patterns (Graumlich 1993a, 1993b, Cook et al. 1991), of fire regime (Swetnam 1993, Swetnam and Betancourt 1990), and of insect outbreaks (Swetnam and Lynch 1993). Research efforts are currently aimed at linking ecosystem processes — productivity, response to climate, etc. — occurring at different spatial and temporal scales (FCCSET 1993).

The development of a forest integrates many environmental factors, hence it is usually difficult to identify the effects of a single phenomenon. For instance, tree mortality or growth decline may be caused by stand dynamics, climatic extremes and/or human modification of the environment (Hyink and Zedaker 1987, NCASI 1990, Oliver and Larson 1990, Bartholin et al. 1992). Site-specific information is usually a major limiting factor in explaining observed growth trends of forest species. As a solution, diverse approaches can lead cumulatively to strong inferential evidence concerning effects of environmental modification on forested areas (McLaughlin and Bräker 1985, Nash 1987). For instance, blending forest mensuration and dendrochronological approaches together is useful for investigating forest ecology problems. Quantitative descriptions of
forest stand dynamics on timescales of decades to centuries rarely include climate as an 
independent variable (Clutter et al. 1983). Dendrochronological techniques maximize the 
climatic signal embedded in annual xylem layers (Hughes 1989), but tree-ring 
chronologies do not necessarily represent total stand growth because of sampling strategy 
and data reduction constraints. Combining forest inventory data with crossdated tree-ring 
records can improve reconstruction and prediction of aboveground tree performance under 
different climatic scenarios.

I.1.1. The target forest type in historical perspective

Ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) is one of the most widely 
distributed *Pinus* species in western North America (Oliver and Ryker 1990). As a 
widespread mid-latitude northern forest, ponderosa pine ecosystems play a role in the 
global carbon budget (Wofsy et al. 1993). Ponderosa pine forests provide critically 
important resources in Arizona, *i.e.* timber, forage, water, wildlife and recreation. Present 
tree cover in this forest type is a mosaic of groups of various ages and sizes. Pines 
within a group are even-aged, although they may vary widely in size (Cooper 1960), or 
uneven-aged, depending on local site conditions, fire and climatic regime (White 1985).

Southwestern ponderosa pine (*Pinus ponderosa* Dougl. ex Laws. var. *scopulorum*) 
stands have changed considerably since European settlement near the end of the 
nineteenth century (Cooper 1960, White 1985). Pre-settlement stand dynamics in this
relatively arid environment were controlled by fire (Weaver 1951, Dieterich 1980). Frequent, low intensity fires spread erratically and burned surface materials without reaching the canopy. Fire controlled the vegetation structure by producing a patchy pattern of surviving trees across the landscape (Moir and Dieterich 1988). Toward the end of the nineteenth century, herbaceous cover alternated with mature and old pines, alone or in clumps of 2–3 individuals, giving an open, park-like aspect to the stand (Pearson 1950). Rare seedlings, saplings and poles occurred in additional small groups. Mortality of old trees was caused primarily by lightning, a frequent phenomenon and a natural cause of fire in the Southwest (Schubert 1974). Pine density in the Flagstaff area averaged 50–60 trees/ha, for a total crown cover of about 20–25% and basal area of 15–20 m²/ha (Covington and Moore 1994, 1992).

Around the 1870s, after Euro-American settlement in northern Arizona, ponderosa pines were cut because of railroad construction, mining operations, and housing development (Schubert 1974). In conjunction with settlement, domestic livestock were introduced in the pine forest. Overgrazing and trampling by cattle and sheep depleted the herbaceous cover and fuels, thereby reducing fire frequency and competition of grasses with pine seedlings (Cooper 1960, Savage and Swetnam 1990). The last spreading fire at Chimney Spring, about 8 km north of Flagstaff, was in 1876 (Dieterich 1980). Serious range deterioration caused by overgrazing in the ponderosa pine forest did not occur until the late 1880s (Dutton 1953). The Beaver Creek Watershed, about 40 km south of Flagstaff, was cited as an example of overstocking, resulting in the "complete annihilation
of pasture in a formerly rich area" (Plummer 1904). Lack of fuels and active fire suppression, which began shortly after 1900 in north-central Arizona (Covington and Moore 1994), reduced the thinning effect that fire once had on pine regeneration (Madany and West 1983). Reduced fire frequency, favorable climatic conditions and good seed crops resulted in abundant pine regeneration during the twentieth century (Pearson 1950).

Today many old-growth ponderosa pine stands are multi-storied, even though age/size classes still occur in a mosaic pattern (Kaufmann et al. 1992a, 1992b). The seedlings that established in the early 1900s have grown into dense pole stands where basal area exceeds 40 m²/ha, density surpasses 2000 stems/ha, and total crown cover exceeds 70% (Covington and Moore 1994, 1992). In such stands, pine crowns have created a patchy but continuous fuel ladder from sapling and pole thickets into the tallest trees. Dead standing pines, snags, and downed logs are common; the herbaceous cover is often sparse or absent. Intra-specific competition for resources reduces growth rates of dominant pines (Schubert 1971, Biondi et al. 1992), making them less responsive to environmental variations, such as an understory burn (Sutherland et al. 1991). This type of old-growth stand is in danger of being destroyed by a high intensity crown fire that kills almost every tree in the stand and creates conditions for a new succession cycle (Moir and Dieterich 1988). Accurate knowledge of spatial and temporal patterns is needed to devise silvicultural guidelines and management decisions for the long-term sustainability of these and other old-growth forests.
1.2. Objectives

The objective of this research was to investigate temporal and spatial trends of aboveground productivity during the twentieth century in an old-growth forest. I intended to reconstruct interannual and decadal patterns of stem increment using a combination of empirical and theoretical approaches. The major question asked was: is it possible to detect growth trends since the early 1900s in a temperate forest ecosystem? I tested the null hypothesis that there was no significant trend. Additional results stemmed from asking the ancillary questions: is there a difference between growth trends of individual trees and of the forest stand they belong to?, or between trees of different size?; and finally, what is the role of climate and competition in shaping the observed growth trends?

I concentrated on a case study in order to maximize the accuracy of results. The study focused on a 800x400-m permanent plot that has been maintained since 1920 in pristine ponderosa pine forest near Flagstaff, Arizona. Available data for the study area included daily meteorological records, repeated forest inventories, and dendrochronological series. The wealth of information available for the field site constituted a unique resource ideally suited for the tasks. Different data sets and analytical approaches provided the integrated framework needed for accurately reconstructing past system behavior.
I.3. **Significance**

This research has both local and global significance. Locally, the study provides a control for silvicultural practices and forest policy. The study documents what happens in ponderosa pine forests when human intervention is limited to fire suppression, which is particularly important for managing old-growth forests in the Southwest. In particular, spatial patterns, temporal growth trends, and mortality rates quantified in this study will help forest and wildlife managers in evaluating current and future strategies to maintain old-growth stands, especially in wilderness areas. Understanding past growth patterns improves prediction of future responses of old-growth ponderosa pine stands in the event of climatic change and/or fire policy modification.

The application of geostatistics to study spatial patterns of tree size and growth represents an innovative use of cutting-edge quantitative methods to address forestry issues. Spatial statistics can help managers to maintain and improve forest stands for long-term sustainability by providing tools to quantify spatial scales of ecological patterns and processes. Spatial knowledge is crucial to define unit areas of forest ecosystems that are homogeneous with respect to a given variable or set of variables. Definition of homogeneous areas leads to designing optimal sampling schemes, applying efficient silvicultural treatments, and reducing management costs, especially in old-growth forests. Investigations on spatio-temporal trends of tree size and increment in natural forests provide information to form the basis of principles to guide general forest management.
for protecting biodiversity and improving long-term sustainability of forests (USDA 1993). For instance, determination of characteristic patterns of old-growth stand structure is useful in enhancing and restoring old-growth ecosystems within managed landscapes (Mladenoff et al. 1993). Furthermore, most ecological theories and models of vegetation composition and productivity assume, explicitly or not, some spatial structuring. Much better simulations and predictions can be obtained by including spatial dependence itself among the predictive variables (Legendre 1993).

This research relates to global change studies on sensitivity and responses of forest ecosystems to modifications of the Earth's atmosphere (FCCSET 1993). Although this is a case study, the results provide valuable input to the analyses of other situations and stress the necessity of multiple viewpoints to capture the multidimensionality of nature. Observational field studies (Cochran 1983, Hurlbert 1984, Eberhardt and Thomas 1991) complement laboratory and manipulative trials in assessing the response of forest ecosystems to global change phenomena. Long-term monitoring of natural phenomena is a fundamental part of scientific discovery (Hofmann 1993, Flueck and Brown 1993). Given appropriate conditions, repeated forest inventories may be used to assess cause-effect relationships (Schreuder and Thomas 1991). Models including both empirical and mechanistic elements are probably best suited for reliable long-term predictions of atmospheric effects on forest growth under changing climatic conditions and/or management strategies (Cook and Cole 1991). Finally, as pointed out in the previous paragraph, this investigation will aid our understanding of the manner in which tree
populations develop at different spatial and temporal scales.

During the last few years, new disciplines — global change studies, Earth system studies, etc. — have emerged whose purpose is to identify cause and effect relationships but without the ability to perform replicable controlled experiments (Schlesinger 1991). In this study, multiple data sets are exploited and compared to reconstruct growth trends from different viewpoints. Tree rings contribute yearly patterns of tree growth, but coarse spatial information on stand development. Repeated forest inventories render decadal patterns of tree and stand growth, and, after stem-mapping, the inventories present spatial patterns of stem size and increment. This interdisciplinary approach makes reconstructed growth trends, as well as their implications, more reliable than in studies based on any single data source.

I.4. Dissertation Overview

With the exception of the introduction and the conclusion, each chapter is written as a self-contained study, closely related to studies described in all other chapters. Figures and tables are placed at the end of the chapter they refer to. Both Chapter II and III present statistical methodology of general value, as well as its application to the study area. Chapter II presents a family of mixed linear models to analyze temporal trends from repeated measurements. The statistical model is applied to the forest inventories to obtain a quantitative, unbiased representation of historical growth trends. Chapter III
illustrates geostatistical models for detecting spatial trends and patterns. Variogram models and ordinary block kriging are applied to inventory data of four stem-mapped plots for quantifying spatial dependence of tree size and increment from 1920 to 1990.

Chapter IV evaluates temporal trends in climatic variables, and illustrates the relationship between climate and tree-ring chronologies from 1920 to 1990. Results obtained in this study are also compared to previous dendroclimatic studies of southwestern ponderosa pine. In Chapter V, temporal trends of tree-ring series are compared to those of forest inventories, and the advantages and disadvantages of both techniques are discussed. Implications of reconstructed growth trends, and recommendations for future research are outlined in the final part, Chapter VI.
II. STATISTICAL TREND DETECTION FROM REPEATED FOREST INVENTORIES

II.1. Introduction

Trees grow in response to the surrounding biotic and abiotic environment and as a function of size and age already attained. In temperate climates, a record of the growth history of an individual tree is contained in its wood layers, produced annually by the vascular cambium. Non-destructive methods to obtain historical information on tree growth from its xylem focus on stem diameter, the easiest tree dimension to measure. Stem diameter, by itself or after transformation into basal area, is closely related to crown size, stem volume and tree biomass (Husch et al. 1982). Traditionally, age-dependent change in size of individual trees and forest stands has been described by means of growth equations (Zeide 1993). Within this framework, growth trends are estimated by fitting a nonlinear function to repeated measurements on each tree or group of trees and comparing the parameters of the fitted equations. Similarly, if polynomials are fitted to the repeated measures, evaluation of trends relies on testing coefficients estimated for individuals or groups (Meredith and Stehman 1991).

Tree age is expensive to measure, hence growth curves usually represent increment as a function of size instead of age. In permanent forest plots, the same subjects are measured repeatedly through time, and analytical models have to consider time-series
variation within subjects as well as cross-sectional variation among subjects (Judge et al. 1985). When growth equations are used, the analysis of these two kinds of variation cannot be performed in a single step. For instance, if the objective is to compare trees by size class at different times, nonlinear models between growth rate and size are fitted at each time, and the estimated parameters are compared for size and time effects. This procedure does not allow an easy definition of the time-series autocorrelation between adjacent times and of the spatial autocorrelation between adjacent trees. Since the form of the growth equation is not known, it is commonly determined from the data, but fitting nonlinear functions with just a few data points per individual can be difficult or unreliable. Poorter and Lewis (1986) discuss additional statistical problems of what they call the 'functional' and 'classical' approaches to the analysis of differences in plant growth rates.

The purpose of this chapter is to present a family of mixed linear models to quantify historical growth trends from repeated measures of permanent plots. Trend is defined as the general, prevailing direction of a statistically detectable change. My objective was to combine the growth history contained in repeated measurements of many trees into a few descriptive parameters that characterize growth of a 'typical' tree in a given time interval for a given size class. The statistical model was designed to test several hypotheses at once, namely how tree growth increment changed by size class and how each size class grew at different time intervals. Since observations are repeated through time on the same individuals, a two-stage model is proposed to consider variation
within a subject at different times — first stage — and across subjects at the same time — second stage. This kind of time-series and cross-sectional data is often called 'longitudinal' in the literature (Goldstein 1979, Plewis 1985). Mixed linear models (Laird and Ware 1982, Ware 1985, Crowder and Hand 1990) are well suited for examining longitudinal data and lead directly to hypothesis tests of model specification. For instance, it is possible to evaluate various error covariance structures (Jennrich and Schluchter 1986) for fixed and/or random effects by means of the Akaike (1974), Schwartz (1978) and log-likelihood ratio tests (Sokal and Rohlf 1981, Wolfinger 1994).

The statistical models presented here are of the following type:

\[ y_{ij} = \beta_0 + \beta_1 x_{ij} + \ldots + \beta_q x_{qj} + b_{0i} + b_{1i}z_{1j} + \ldots + b_{ri}z_{rj} + e_{ij} \]

where

- \( y_{ij} \) = j-th univariate measurement made on the i-th individual;
- \( \beta_0 + \beta_1 x_{ij} + \ldots + \beta_q x_{qj} \) = fixed effects for the j-th measurement;
- \( b_{0i} + b_{1i}z_{1j} + \ldots + b_{ri}z_{rj} \) = random effects for the j-th measurement made on the i-th individual;
- \( e_{ij} \) = error term for the j-th measurement made on the i-th individual.

Fixed effects represent the mean level of \( y_{ij} \) over all i-th individuals. Random effects represent the mean difference, for the i-th individual, between \( y_{ij} \) and the overall mean level. The error term represents the difference between \( y_{ij} \) and its mean value computed
from fixed and random effects. In matrix form, the model can be written as follows:

\[ y = X \beta + Z b + e \]

with the following expectations \((E)\), variances \((V)\), and covariances \((CoV)\):

\[
E(e) = 0 \quad E(b) = 0 \quad E(y) = X \beta
\]

\[
V(e) = R \quad V(b) = G \quad CoV(b, e) = 0 \quad V(y) = Z G Z^T + R
\]

This general model is adequate for measurements that are both heteroscedastic and autocorrelated because it models not only the mean of \(y\) but also its variance (SAS Institute 1992). Hence, the model allows various types of correlation within subjects (time-series autocorrelation) and across subjects (spatial autocorrelation), as well as the existence of missing observations. For statistical tests, normality is assumed for \(b_i\) and \(e_i\) — and consequently for \(y_i\).

Time-dependent trends are not easily quantified. The models presented here enjoy simplicity because a specific functional form for growth curves need not be specified, and generality because the model fits a parameter for each growth increment, and thus every growth function is a special case of these models. In addition, if environmental effects and treatment factors are included in the model, it is possible to quantify and test their significance in a single step. Suppose we let \(y_{ij}\) be the incremental growth measurement taken at the \(j\)-th time period on the \(i\)-th tree. One simple version of the model assumes that \(y_{ij}\) depends on the size of the tree at the beginning of the time period, and on an environmental effect due to the time period. Suppose that size is classified into \(S\) classes, and that data have been recorded for \(T\) time periods. Some trees may have been observed...
for fewer time periods, and some may have missing data. The linear model for the $j$-th observation, $j = 1, \ldots, T$, on the $i$-th tree, $i = 1, \ldots, n$, can be written as (Freund and Littell 1981):

$$ E(y_{ij}) = \mu + s_{ij} + t_j + (st)_{ij} $$

where $E$ denotes expectation, $\mu$ is the reference value, $s_{ij}$ is the size-class effect for the $i$-th tree in the $j$-th period, $t_j$ is the effect of the $j$-th time period, and $(st)_{ij}$ is the interaction effect. The errors, $e_{ij}$, are assumed to be normally distributed with zero mean. Within a tree, the errors are correlated, with covariance matrix given by $V(e_i) = R$. The covariance within a tree is assumed to be the same for all trees. The matrix $R$ could be completely unstructured or have a specified structure, such as first-order autoregressive (Pindyck and Rubinfeld 1981) or Toeplitz (Press et al. 1988). The model assumes that the trees in the sample are independent, and does not consider any spatial autocorrelation, although it could be extended to allow for this as well.

This simple model can easily be made more elaborate, and realistic, by adding additional factors and their interactions (Moser et al. 1990). For instance, if a competition index were computed for each tree at each measurement time, then a competition factor could be added to the model. If treatments or management strategies were applied to the trees, then a factor for treatment or management could be added. Given a sample of $n$ trees, Jennrich and Schluchter (1986) provide general methodology for obtaining maximum likelihood estimates of model parameters. Their methodology has been implemented in the SAS procedure Proc Mixed (SAS Institute 1992, Wolfinger 1994), and
I employed that software for fitting the model to a real-life data set. Individual tree characteristics changed through time and comparisons had to be made between different size classes and time periods. When historical trends and patterns are of interest, the major advantage of applying mixed models for longitudinal data to forest inventories is to perform the analysis on all trees and time intervals at a stroke (Eriksson et al. 1990).

II.2. Materials and methods

II.2.1. Study area

The Gus Pearson Natural Area, located along U.S. Highway 180, about 15 km northwest of Flagstaff, Arizona, is one of the first Research Natural Areas established in the United States of America (Avery et al. 1976). It is included in the Fort Valley Experimental Forest, within the Coconino National Forest, Coconino County. Established in 1908, Fort Valley was the first forest experiment station in the United States (Schubert 1974). Geographical coordinates for the approximate center of the area are 35°16′11″ N and 111°44′30″ W; elevation is 2230–2260 m. The southwestern corner of the Gus Pearson Natural Area has UTM coordinates of 432243 (easting) and 3902810 (northing) in zone 12. Climate, topography, soil parent material and soil type, biota and disturbance history are homogeneous over the entire area (Avery et al. 1976, White 1985). Climatic regime is described in detail in Chapter IV. Topography is level to gently undulating,
with an average slope and exposure of about 5% and 182°, respectively. Bedrock is formed by basaltic lava flows of late Tertiary origin, and soils consist of montmorillonitic clay-loams with high moisture-holding capacity. Small rock outcrops are present, but the area has the potential of being fully covered by trees (Avery et al. 1976).

The Gus Pearson Area is an uneven-aged, pure, old-growth stand of southwestern ponderosa pine (Pearson 1950). It is an 800x400-m permanent plot divided in 29 100x100-m subplots plus five smaller subplots. Plots 1–29 were neither thinned nor burned during the period covered by the forest inventories. Plots 30–34, the ones closest to the Fort Valley Experiment Station, have been thinned in the past, and were therefore excluded from the analysis. During the first inventory, in 1920, all pines with diameter at breast height (1.3–1.5 m; DBH) above 8.9 cm (3.5") were marked by means of a metal tag with plot and tree number. The Forest Service has remeasured stem diameter at tag level every five years from 1920 to 1960, and every ten years from 1960 to 1990.

The 1920–1970 inventories of plots 1–14, 16 and 27 have already been published (Avery et al. 1976). On those plots, ingrowth was measured from 1925 to 1960 by placing new tags on pines whose DBH had exceeded 8.9 cm since the last inventory. In 1970, the minimum diameter for inclusion in the inventory was raised to 15.2 cm (6") and ingrowth was measured only on plots 15, 17, 23–26 and 28–29, where ingrowth had not been measured since 1940. Because of budget constraints, no ingrowth was measured in 1980 and 1990. Three different kinds of tags can still be found on some large trees: current tags were first used in 1970. At that time, pines already dead were given the last
numbers for the plot and their original number was assigned to a new, nearby tree. Although this does not affect the data, it makes it impossible to obtain coordinates of trees that died before 1970.

At present, the inventory database includes up to 12 DBH measurements per tree, repeated throughout a 70-year period on a total of 5,724 pines. Data were converted from English to metric units and checked for errors and inconsistencies. Stem basal area (BA, cm$^2$π$^{-1}$) and 10-year periodic basal area increment (PBAI, cm$^2$π$^{-1}$) were computed from the repeated measurements of stem diameter (DBH, cm). Negative PBAI values were used to identify data entry errors. When either the 5-year PBAI exceeded 100 cm$^2$π$^{-1}$ or the 10-year PBAI exceeded 200 cm$^2$π$^{-1}$, the corresponding DBH values were critically evaluated. Pre-1980 DBH values on plots 1–14, 16 and 27 were compared with values listed in Avery et al. (1976). Whenever possible, pines with abnormal 1990 DBH were inspected in the field. If a pine was missing in 1980 and measured in both 1990 and 1970, the missing value was estimated.

Ingrowth, outgrowth, and mortality — as defined by Beers (1962) — were computed at 10-year intervals for the 1920–1990 period. Results were tabulated and charted for different size classes, years and/or plots. Computations were checked using the following formula:

$$n_{ts} = (n_{t-1} - o_t + i_t - m_t)$$

where $n_{ts} =$ number of trees in size class $s$ at time $t$; $n_{t-1} =$ number of trees at time $t-1$;
\( o_t \) = outgrowth at time \( t \), \( i.e. \) trees that grew into a larger size class between time \( t-1 \) and \( t \); \( i_t \) = (for the smallest size class) ingrowth at time \( t \), \( i.e. \) trees entered in the inventory between time \( t-1 \) and \( t \); \( o_{t, i-1} \) = outgrowth at time \( t \) from the next smaller size class; \( m_t \) = mortality at time \( t \), \( i.e. \) trees that died between time \( t-1 \) and \( t \). At first, only two size classes were considered: (1) DBH < 50.0 cm ('blackjacks', 'young' or 'small' pines), (2) DBH \( \geq \) 50.0 cm ('yellow', 'old' or 'large' pines). This division is common in forest management of ponderosa pine (Schubert 1974). A second set of size classes was defined to increase resolution of results: (1) DBH < 30.0 cm ('blackjacks', 'young' or 'small' pines), (2) 30.0 \( \leq \) DBH < 50.0 cm ('yellow', 'old' or 'large' pines). This second set divides the range of DBH in the inventories, from about 10 to about 110 cm, into 5 classes of equal width.

Trends in tree size (basal area) and growth rates (10-year periodic basal area increment) were analyzed by size class, graphically and numerically. The nonparametric, univariate Mann-Kendall test (Kendall and Gibbons 1990) was used to evaluate monotone temporal trends. Size classes were applied to all pines measured on plots 1–29 — the number of observations ranged from 2,519 in 1920 to 5,481 in 1970 — as well as to two subsets independent of ingrowth records. The first subset was formed by the 2,519 pines present at the beginning of the observation interval, in 1920. The second subset consisted of a stratified random sample of 58 pines present at the end of the observation interval, in 1990. On each plot, two pines were randomly selected, one above and one below 50-cm DBH. Using all available observations is necessary to obtain trends for the entire
Because of changes in minimum size requirements and tagging procedures, the analysis of the two subsets provides the best results for trends within individual trees. Time-series charts for the 58 pines represented individual tree values, whereas charts for all pines depicted plot values. Statistical models always referred to individual trees. A third subset, formed by the 2,077 pines always present from 1920 to 1990, was considered. Since results obtained using the first and the third subset were indistinguishable, discussion was limited to the first two subsets.

II.2.2. The Statistical Model

For quantitative description of temporal growth trends in individual trees I employed a mixed linear model of repeated DBH measurements. I assumed that tree growth in a given time interval could be divided into two major components: (1) an internal, time-varying component associated with the size of the tree; (2) an external, time-varying component that includes all time-varying environmental factors that apply to the tree in a given time interval. Individual tree effects are random, whereas size and time effects are fixed. Plots were not included in the model because they define land units that do not differ in terms of vegetation forming factors (Major 1951). The time effect characterizes temporal variation and helps to understand the effects on tree growth of long-term environmental changes that influenced tree growth over the observation period. The time effect was expressed by seven classes: (1) 1920–30, (2) 1930–40, (3)
1940–50, (4) 1950–60, (5) 1960–70, (6) 1970–80, (7) 1980–90. Size was divided into a few non-overlapping size classes, as described in the previous section.

Growth increment of individual pines, the response variable, was quantified as 10-year periodic basal area increment (PBAI), as follows:

\[
PBAI_i = \frac{\left( DBH_i^2 - DBH_{i-10}^2 \right)}{4}
\]

with \( t \) = year of the forest inventory. The mixed linear model was estimated as follows:

\[
\text{Expected growth increment} = \text{Size} + \text{Time} + (\text{Size} \times \text{Time interaction})
\]

After testing significance of the main effects and their interaction, the model was re-estimated as

\[
\text{Expected growth increment} = (\text{Size} \times \text{Time interaction})
\]

to accurately compute standard errors of the seven different time slopes for each size. Slope estimates were plotted against time to represent a synthetic, accurate description of temporal growth trends for each size class (Poorter and Lewis 1986, Weisberg 1993). A multitude of contrasts among slope parameters could be devised to test differences in growth increments, but only the most interesting hypotheses were actually tested.

Assumptions had to be specified for independence, autocorrelation and normality (Weisberg 1985). If random samples are taken from all available trees, such as the 58-pine subset, the assumption of independence will generally hold. If all available trees are included in the analysis, growth increments may be spatially autocorrelated. Spatial
autocorrelation was investigated by stem-mapping tagged pines on a 100x400-m area formed by plots 5, 12, 13 and 20. Geostatistical models indicated that spatial autocorrelation of 10-year periodic basal area increment was small and practically disappeared after about 1950 (Chapter III). Growth increments within a tree are temporally autocorrelated. Hence, both a first-order autoregressive, or AR(1), and a Toeplitz covariance structure were used to model the R matrix (SAS Institute 1992). Toeplitz matrices have constant upper-left to lower-right diagonal elements and have been used extensively in areas of pure and applied mathematics since the beginning of this century (Heinig and Rost 1984, Vautard et al. 1992). Model performance and deviations from normality were evaluated by numerical and graphical analysis of model residuals (Neter and Wasserman 1974).

After defining temporal trends using models (1) and (2), an attempt was made to incorporate a density factor. Since the only spatial information available on a pine was its plot number, each pine within a plot had to be scaled against the whole plot. This procedure is inaccurate because point density changed considerably within a plot (Chapter III), but the purpose of the exercise was to show how easily an additional factor could be included in the model. Glover and Hool (1979) proposed the following index:

\[ DI_{kj} = DBH_{kj}^2 \left( \frac{n_j^2}{\sum_{i=1}^{n_j} DBH_{ij}} \right) \]

where \( DI_{kj} \) = density index for pine \( k \) within plot \( j \); \( DBH_{kj} \) = stem diameter of pine \( k \).
within plot \( j \); \( n_j \) = number of pines on plot \( j \), including pine \( k \); \( DBH_{ij} \) = stem diameter of pine \( i \) within plot \( j \). This index scales the size of each tree relative to the average size of all trees on the plot. It was designed for loblolly pine plantations monitored over one time interval where tree density could only decrease because of mortality. Here the index is expressed in terms of stem DBH, but it was originally proposed in terms of stem basal area.

In this study, ingrowth could decrease average stem size on a plot even though plot density increased. Therefore, the size of each tree was scaled against the total size of all trees on the plot, as follows:

\[
DI_{ij} = DBH^2_{ij} \frac{100}{n_j} \frac{1}{\sum_{i=1}^{n_j} DBH^2_{ij}}
\]

This new index maintains Glover and Hull’s original idea of using basal area instead of DBH to express relative tree size. The idea of scaling the size of the subject tree against the cumulative size of the surrounding trees is also found in Lorimer’s (1983) index, which correlated well with mean growth rates of southwestern ponderosa pine in northern Arizona (Biondi et al. 1992). The expanded model was estimated as follows:

\[
\text{Expected growth increment} = \text{Size Effect} + (\text{Size} \times \text{Time interaction}) + \text{Density Effect} + (\text{Size} \times \text{Density interaction}) + (\text{Time} \times \text{Density interaction})
\]

The density effect is continuous and is expected to be positive in sign because both growth increment and density index should decrease with increasing density. This model
could determine not only size and time effects but also how tree growth changed with density. Custom linear contrasts could detect the time intervals when density was most important for tree growth, as well as the size classes that were most affected by density.

II.3. Results and Discussion

II.3.1. Exploratory Data Analysis

Data quality verification resulted in a total of 198 corrections made on 109 pines, corresponding, respectively, to 0.4% of all non-missing observations and 1.9% of all pines included in the forest inventories. Of the initial 2,519 pines present in 1920, 442 died over the observation period, leaving 2,077 pines always present from 1920 to 1990. A total of 3,205 pines entered the inventory from 1925 to 1970, but 115 of them died from 1935 to 1990. The 1990 inventory included (2,519−442+3,205−115)=5,167 pines still alive. Maximum stem size ranged from 107.7 cm in 1920 to 114.3 cm in 1990, and was always recorded on the same pine. Maximum tree age was greater than 600 years in 1990, because the largest number of annual rings counted on a single increment core was 615. Detailed information on the oldest pine, which was not the largest one, is given in Chapter IV.

Frequency distributions of stem DBH changed through time. When all available observations were used, skewness to the right increased through time (Figure 1), mostly
because of large numbers of small pines being added at each inventory from 1925 to 1970. When observations were restricted to pines present in 1920, histograms of stem DBH showed an opposite trend, particularly after 1950 (Figure 1). At the beginning of the observation period, in 1920, the pine stand was mostly a two-story forest, with groups of small trees in the understory and groups of large trees in the overstory. As time passed, successful regeneration pulses changed the structure of the stand to a multi-storied one, composed by a mixture of uneven-aged groups of pines, each group formed by roughly even-sized individuals. Although stand density increased, the average horizontal dimension of pine groups remained about 30 m from 1920 to 1990 (Chapter III).

The large number of small pines present in 1920 ranged in size from 9 to 25 cm, the mode being 10–12.5 cm (Figure 1). Ponderosa pine in the Flagstaff area usually reaches breast height after 10–25 years (Minor 1964). According to Cooper (1960), it takes at least 20 years for the average pine to reach 10-cm DBH. Presumably, the strong regeneration pulse responsible for the large number of small pines present in 1920 occurred in the last decades of the 1800s. Pearson (1950, p. 117) suggested that the early 1880s were years of abundant and successful pine regeneration. Given the introduction of livestock grazing and the lack of spreading fires in those decades, it is likely that reduction of herbaceous competition favored the establishment of pine seedlings, and that absence of fire-related thinning let seedlings grow into larger size classes. The second mode in the 1920 histogram corresponds to pines with 40–60 cm DBH (Figure 1). Age of those pines is likely to be between 100 and 200 years, which would agree with the
abundance of pine regeneration at the turn of the nineteenth century identified by White (1985).

Repeated photographs of the pine forest in 1909, 1938, 1944, 1949, 1990, and 1992 document the increased stand density. These photos were taken on the east edge of plot 17, and three of them have recently been published (Covington and Moore 1994). Pine regeneration is first evident in the 1938 photo, and, given the size of seedlings and saplings, it most likely originated in 1919, when unusually abundant and widespread reproduction occurred over most of the Colorado Plateau (Pearson 1950, Schubert 1974). In the 1909 photo, which was first published by Pearson (1931, p. 8), the forest cover is devoid of herbaceous species. This, combined with the lack of spreading fires since 1876 (Dieterich 1980), supports accounts of overgrazing in the Flagstaff area during the 1880s, with long-lasting range damage mostly caused by sheep browsing (Cooper 1960). Schubert (1974, p. 18) maintains that herbaceous ground cover is often inhibited by competition for moisture between large pines. This belief, however, is in contrast with the description of pre-settlement pine forests as open, park-like, and with abundant grass cover. According to Cooper (1960), herbaceous vegetation disappears when pine crown cover exceeds 75%.

Ingrowth includes the trees that periodically grow into the smallest measured size class of a forest stand (Husch et al. 1982). It is the direct outcome of successful tree regeneration, a highly variable process (Shifley et al. 1993). Since no information was available between inventories, the size of incoming trees was defined by their first
measured DBH. Ingrowth was not recorded in 1980 and 1990. From 1925 to 1970, ingrowth fluctuated around a linear trend with positive slope (Figure 2). The large influx of new pines between 1940 and 1950 was most likely related to the "excellent 1919 seedling crop over most of the Colorado Plateau" (Schubert 1974, p. 12). Successful regeneration may have occurred at other times, as "good cone crops [for the 1908–1973 period] were reported on the Coconino and Kaibab National Forests in 1908, 1913, 1918, 1927, 1931, 1936, 1942, 1945, 1954, 1956, 1960, 1965, 1968, and 1971" (Schubert 1974, p. 42). At Fort Valley, from 1909 to 1945, exceptional seedling establishment was observed only in 1919, good establishment in 1914 and 1929, and some establishment in 1909, 1911, 1917, 1921, and 1937 (Pearson 1950, p. 117). Because of inconsistent tagging procedures and increased minimum size requirements, ingrowth data were not very reliable after 1940. This affects the number of available observations, which either did not increase as much as it should have or increased suddenly instead of smoothly (Figure 3). Ingrowth until 1970 consisted of pines with DBH below 30 cm (Figure 2), hence the number of available observations for size classes above 50-cm DBH remained accurate from 1920 to 1990.

Stand density was defined by the number and basal area of pines measured at each inventory. A constant, 29-ha area formed by plots 1–29 — each plot 100x100 m in size — was considered through time. Hence entire-area values, instead of unit-area values, were used to represent historical trends. Density was computed by size class and for the whole size range (Table 1). Density values for pines with DBH ≥ 50.0 cm were
reliable from 1920 to 1990, but density data for pines with DBH < 50.0 cm depend on accuracy of ingrowth records, hence they underestimated true values, especially after 1970. Stand density increased linearly through time from 1920 to 1970 (Figures 4 and 5, Table 1). The Mann-Kendall test for stand density and basal area was positive and significant for all size classes — 0.005 ≤ p-value ≤ 0.056. The number and basal area of pines with DBH ≥ 50.0 cm increased slowly from 1920 to 1970, then decreased from 1970 to 1990 (Table 1, Figure 6). As explained in the following paragraphs, increased mortality and decreased outgrowth were responsible for this recent downward trend. When computed from 1920 to 1990, the Mann-Kendall test for stand density and basal area was not significant for size classes 3, 4, and 5 — p-value ≥ 0.216. The number of pines with DBH < 50.0 cm increased almost exponentially from 1920 to 1970 (Figure 6). Lack of ingrowth records and increased mortality were responsible for the largely artificial downward trend from 1970 to 1990 (Figure 6). Stand basal area of pines below 50-cm DBH increased steadily from 1920 to 1990 (Figure 6), although data underestimated true values, especially after 1970.

Relative variability of DBH in any given year, as measured by the coefficient of variation (Sokal and Rohlf 1981), decreased from size class 1 to size class 5 (Table 1). This happened because average DBH increased by definition from size class 1 to size class 5, but the standard deviation remained fairly constant across size classes. The coefficient of variation for all available DBH observations increased from 1920 to 1960 (Table 1), mostly because the average DBH decreased more with time than the standard
deviation. From 1960 to 1990 the coefficient of variation decreased (Table 1), mostly because average DBH increased with time and the standard deviation decreased. Lack of ingrowth observations was most likely responsible for the last downward trend in overall relative variability of stem DBH.

Mortality includes trees that die between two consecutive inventories. Since no information was available between inventories, the sizes of pines that died were quantified by their last measured DBH. Lack of complete ingrowth records did not affect mortality computed for large pines, but it probably caused an underestimation of mortality among small pines, especially after 1970. In terms of absolute numbers, mortality of small and large pines followed similar temporal patterns (Figures 7 and 8), which were consistent when computed using all available observations or only observations on pines present in 1920 (Figure 7). Pine mortality increased from 1930 to 1960, was lower in 1960–70 and much higher in 1970–80, then lower again in 1980–90. The reduction in mortality from 1970–80 to 1980–90 was more pronounced among large pines (Figure 8).

When mortality was computed as percentage of stand density at the start of the 10-year interval (Figures 9 and 10), it was evident that mortality increased with tree size. At all times, mortality of large pines was much higher than mortality of small pines (Figure 10). The former increased over time — the Mann-Kendall test had p-value = 0.051 —, whereas the latter did not — the Mann-Kendall test had p-value = 0.348. The most likely culprit for the positive temporal trend in mortality of large pines is greater competition for resources generated by increased crowding, especially because no
widespread mistletoe, limb rust, root or stem rot, needle blight, pine beetle or defoliator attack could be identified in the field and from analysis of tree-ring samples (Chapter IV).

Outgrowth is the direct outcome of survivor growth (Husch et al. 1982). It includes the trees that periodically grow into a larger size class. Since no information was available between inventories, outgrowing pines were defined by their DBH at the beginning of each period, and were referred to the size class from which they originated (Table 2). Therefore, pines outgrowing the 50-cm DBH boundary (Figure 11) were represented by outgrowth values for size class 2. By definition, outgrowth was null for the largest size class (Table 2, Figure 12). Outgrowth data for size classes 2-4 were reliable from 1920-30 to 1980-90, but data for the first size class were affected by ingrowth records, and underestimated true values, especially after 1970. The artificially increasing outgrowth from size class 1 after 1970 was prominent when outgrowth was computed as percentage of stand density at the beginning of the 10-year interval (Figure 12).

The number of pines growing from class 2 to class 3 decreased through time (Table 2, Figures 11-13), even though the number of pines in size class 2 increased through time (Table 1). Evidently, the average growth rate of surviving pines decreased with time as a reflection of increased stand density and greater competition for resources. Repeated feeding by Abert’s squirrels may reduce growth rates of ponderosa pines in the Colorado Front Range, but this reduction is limited to isolated individuals, not to an entire stand (Snyder and Linhart 1993). By comparing outgrowth from size class 2 with
mortality of pines greater than 50-cm DBH (Figure 13), it was possible to notice that the balance between recruitment and mortality of large pines was positive from 1920 to 1970 — thus density of large pines increased —, and negative from 1970 to 1990 — thus density of large pines decreased (Table 1).

Total periodic basal area increment (TPBAI) was computed by size class (Table 1), which was defined by stem DBH at the beginning of the period. Hence, the value of 4.0 m²·t⁻¹ reported in the first row of the TPBAI column (Table 1) represents the increment from 1920 to 1930 of pines that in 1920 were in size class 1 and did not die before 1930. Because of ingrowth, values of TPBAI computed using all available observations (Table 1) differed from those computed using only pines present in 1920 (Table 3). This difference was limited to size class 1 from 1930-40 until 1950-60, and to size class 1 and 2 from 1960-70 to 1980-90. Lack of ingrowth records, especially after 1970, underestimated TPBAI for the entire stand (Table 1), but did not affect validity of TPBAI values for the pines present in 1920 (Table 3).

Total periodic basal area increment (TPBAI) of the entire stand remained fairly constant through time (Figure 14, Table 1). The Mann-Kendall test applied to TPBAI values from 1920 to 1990 (Table 1) was positive for size class 1 — p-value = 0.033 — and negative for size classes 3 and 4 — p-value = 0.004 and 0.015, respectively. For the stand as a whole, TPBAI showed no significant trend either from 1920 to 1970 or from 1920 to 1990 — the Mann-Kendall test had p-values ≥ 0.453. Visual inspection of time-series charts based on plot values computed using all available observations (Figures 14,
16 and 18) or only observations on pines present in 1920 (Figures 15 and 17) indicated that growth rates of individual pines decreased with time regardless of their size in 1990. Ingrowth compensated for this downward trend by adding new individuals in the smallest size classes (Table 1, Figure 16). When only pines present in 1920 were considered, the downward trend of 10-year periodic basal area increment (PBAI) occurred in all size classes (Table 3).

The decrease through time of individual growth rates changed the frequency distributions of periodic basal area increment (PBAI). As growth rates of more and more pines declined with time, the PBAI frequency distributions became more and more skewed to the right (Figure 19). This was also true when all available observations were used, although the distribution of growth rates, especially after 1970, was affected by lack of ingrowth data. When only the 58 cored pines were considered, their individual growth rates showed a difference between large and small pines. Pines with 1990 DBH ≥ 50 cm showed a downward trend in PBAI with time (Figure 20), but pines with 1990 DBH < 50 cm did not (Figure 21). Not surprisingly, statistical models were needed to provide an unbiased and accurate description of temporal growth trends by size class.

II.3.2. Statistical Trend Detection

Mixed linear models fitted to the data gave consistent results. As mentioned in the methods, three subsets of all available observations were used to ensure that the data
were independent of ingrowth records, and every subset gave similar results. For brevity, reported findings pertain to the random sample of 58 pines selected at the end of the 1920–1990 period, and to the population of 2,519 pines present at the beginning of that interval. Models based on size and time effects and/or size-time interaction were always highly significant. The Akaike, Schwartz and log-likelihood ratio tests indicated that, for a given error covariance structure, mixed linear models performed better with five size classes than with two size classes. The same tests indicated that, for either two or five size classes, the Toeplitz covariance structure performed better than the first-order autoregressive covariance structure. Hence, discussion of results is limited to models with five size classes and Toeplitz covariance. When a density index was added to the model, density effects were significant only for the smallest size class. Because of inaccuracy in the density index itself, results of this expanded model were deemed unreliable and discussion is limited to models without the density index.

Graphical analysis of model residuals did not indicate strong deviations from normality assumptions, especially for the random sample (Figure 22). Parameter estimates for the pines originally present in 1920 were used to represent the ‘typical’ growth rates of pines in a given size class and time interval (Figure 23, Table 4). A total of 16,280 degrees of freedom was available, as given by the number of pines — 2,519 — times the number of repeated measurements — 7 — minus the number of missing values — 1,318 — and minus the number of slope parameters — 35. All parameter estimates were highly significant (p-value < 0.001), with the sole exception of that for

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size class 5 in period 1970–80 (p-value = 0.566, Table 4). Based on standard errors of parameter estimates, variability of growth rates for a given size class did not change much through time. However, some differences existed between size classes at a given time. Growth rates of pines in size class 1, 2 and 3 had standard errors that were 30–40% smaller than those of pines in size class 4, and growth rates of pines in size class 4 had standard errors that were 60–70% smaller than those of pines in size class 5 (Table 4, Figure 23). The larger variability of pines in size classes 4 and 5 was probably the result of smaller sample sizes (Table 3).

Periodic basal area increment declined in all size classes over time, but the decline changed from one size class to another and from one time interval to another (Table 4, Figure 23). Linear contrasts were used to assess significance of differences between parameters. Regardless of size class, growth rates in 1920–30 were significantly (p-value < 0.001) greater than those in 1950–60, which were significantly (p-value < 0.001) greater than those in 1980–90. However, the order of growth rates, by size class, reversed during the observation interval. In 1920–30, growth rates of small pines were significantly (p-value < 0.001) lower than those of large pines, as follows:

1920–30: (size 1) < (size 2) < (size 3, size 4, size 5)

After 1920–30, growth rates of large pines declined faster than those of small pines, and in 1950–60 the order reversed, with small pines growing significantly (p-value < 0.001) faster than large pines, as follows:

1950–60: (size 1, size 2) > (size 3) > (size 4, size 5)
In the last decades, the decline continued, but the order established in 1950–60 remained unaltered. Growth rates in 1980–90 had exactly the same order as in 1950–60, i.e. trees below 50-cm DBH had the highest growth rates and trees above 70-cm DBH had the lowest ones. Because of mortality and outgrowth, pines included in a given size class could change over time. Hence, model results do not refer to the age-related development of the same trees; they rather quantify the performance, during a defined time interval, of a ‘typical’ tree of specific size.

II.4. Conclusions

Forest inventories, repeated at 10-year intervals from 1920 to 1990, showed that tree density and stand basal area increased, periodic basal area increment of the whole stand was stationary, growth rates of individual trees declined regardless of size class, and mortality increased, especially among the largest trees. The constant increment of total stand basal area from 1920 to 1990 indicates that the pine population as a whole has not yet reached its ‘carrying capacity’, i.e. the limit imposed by available resources (Silvertown 1987). Further research, based on tree biomass rather than tree basal area, is needed to clarify stand dynamics in the absence of fire. For instance, the prolonged, unusual, lack of fire during the twentieth century may be driving a transition from a fire-controlled ecosystem, where no self-thinning occurred, to a density-controlled ecosystem, where the -1.5 power law and de Liocourt’s law (Harper 1977) both apply. The incline
of mortality from 1920 to 1990 suggests that, as the stand approaches its maximum biomass, population processes become progressively more controlled by density-dependent mechanisms. Preliminary observations indicate self-thinning within the dense groups of small pines, but the increased mortality and reduced growth rates of large pines contradicts the -1.5 power law, and it deserves additional investigation.

The possibility of quantitative comparisons between parameter estimates is the most important advantage of using a mixed linear model to estimate temporal trends. Visual patterns can be statistically tested, resulting in accurate specification of time-dependent growth patterns. Whenever sample sizes are large, the model presented here is an ideal tool to summarize individual growth patterns over time. Once an accurate description of historical trends has been obtained, identification of forcing factors becomes easier. In the study area, temporal trends identified by the model are not solely explainable by size differences. Growth rates of pines declined regardless of tree size, and growth rates of large pines declined more than those of small pines. At the beginning of the observation interval, from 1920 to 1930, large pines were growing faster than small pines. At the end of the observation interval, from 1980 to 1990, large pines were growing slower than small pines. Since the number of small pines almost tripled over the observation period, whereas the number of large pines increased slightly, it is possible to conclude that, other factors being equally important among size classes, competition for resources was more detrimental for large pines than for small pines.

Temporal growth trends were quantified using a statistical model to minimize bias
and subjective judgement of graphical displays. However, if the observed growth trends were caused by competitive interactions alone, they should be reconciled with established ecological theory. Competition between plants is usually defined as a reciprocal negative interaction mediated by the mutual exploitation of shared resources (Connell 1990, Bazzaz and McConnaughay 1992). Negative interactions among plants are then divided in three categories based on the relationship between competitive ability and plant size. In symmetrical interactions plant size does not determine competitive ability, in size-symmetrical interactions competitive ability is directly proportional to plant size, in asymmetrical interactions plant size and competitive ability are positively but nonlinearly related. Results presented in this chapter indicate that competitive ability was inversely related to plant size. A large tree grew faster than a small tree when stand density was low; when crowding increased, a large tree grew slower than a small tree. This result escapes all the above mentioned categories.

De Wit (1960) proposed to use 'competition for space' as a combination of all plant interactions for growth-limiting factors. From this point of view, the three-dimensional space available to large and small trees, above and below ground, changed over time. The exponentially increasing density of small pines reduced the space available to large trees, especially below ground. Even though it is impossible to know the exact mechanisms, the influence of competition on growth rates probably concentrated on the amount of soil occupied by roots of large and small pines. Differences in age-related vigor may also make the large, old trees more susceptible to intra-specific
competition than the small, young trees. It is remarkable that the growth decline of large pines was predicted long ago. According to Pearson (1950, p. 67–68)

"The reason for the good growth of large trees in the virgin stand is that most of them were partially isolated. But now that reproduction has come in, young trees will claim an ever increasing share of the limited moisture supply which the veterans were able to monopolize as long as fire and grazing prevented regeneration. It is to be expected that another 20 years will witness a marked decline in the growth of large trees".

An important conclusion of practical interest to forest managers can be drawn from this study, especially considering how mortality of large pines increased through time with increased stand density. If old-growth ponderosa pine ecosystems are to be maintained, large trees need to be spared from excessive competition with smaller trees. Before European settlement, frequent low-intensity fires regulated stand density. Nowadays the vicinity of developed areas and the amount of fuel accumulated on the ground inhibits prescribed burning in many ponderosa pine forests. In such cases, Covington and Moore (1992, p. 81) pointed out that "to maintain a viable cohort of old-age class trees, it may well be necessary to thin out most of the postsettlement trees, manually remove heavy fuels from the base of large, old trees, and reintroduce periodic burning".
FIGURE 11.1. Histograms and box plots of stem diameter (DBH) measured at three different times on all tagged pines ('ALL PINES' column) and on pines first inventoried ('1920 PINES' column). The number of observations (N) is given in each histogram. The x-axis scale is constant for all histograms, the y-axis scale is constant for histograms in the same column. The 2,077 pines included in the lower-right histogram were always present from 1920 to 1990.
ALL PINES

1920 PINES

<table>
<thead>
<tr>
<th>Year</th>
<th>Frequency</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>1920</td>
<td>1000</td>
<td>2519</td>
</tr>
<tr>
<td>1950</td>
<td>1000</td>
<td>4180</td>
</tr>
<tr>
<td>1990</td>
<td>1000</td>
<td>5167</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Year</th>
<th>Frequency</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>1920</td>
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<td>2519</td>
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<td>1950</td>
<td>300</td>
<td>2425</td>
</tr>
<tr>
<td>1990</td>
<td>300</td>
<td>2077</td>
</tr>
</tbody>
</table>

DBH (cm)
FIGURE II.2. Time-series chart of pine ingrowth recorded at 10-year intervals, from 1920–30 to 1960–70. The chart shows the total number of new pines (N) and their minimum (MinD), median (MedD), and maximum (MaxD) diameter.
FIGURE II.3. Time-series chart of the number of tagged pines on plots 1–29. The chart illustrates how tagging procedures influenced the number of available observations (see text for details).
FIGURE II.4. Time-series chart of the total number (N) and basal area (BA) of tagged pines. The chart can be used to approximate increased pine density with time. The dotted vertical line highlights the lack of ingrowth records after 1970.
FIGURE II.5. Time-series chart of the total basal area (TBA) of tagged pines on plots 1–29. The dotted vertical line highlights the lack of ingrowth records after 1970.
FIGURE II.6. Bar chart of the total number (ND, Nd) and basal area (BAD, BAd) of tagged pines above (ND, BAD) and below (Nd, BAd) 50-cm DBH. The chart can be used to approximate changes in pine density with time. The dotted vertical line highlights the lack of ingrowth records after 1970.
Bar chart of pine mortality, i.e. the number of pines that died within a given time interval. Mortality values are charted by size class (1,2,3,4,5 and TOT, which represents all sizes) and by 10-year interval, from 1920–30 to 1980–90. Note that differences between mortality values computed using all available observations ('ALL PINES' row) and using only observations on pines first inventoried ('1920 PINES' row) are restricted to size class 1 from 1920–30 to 1950–60, and to size classes 1 and 2 from 1960–70 to 1980–90.
FIGURE II.8. Time-series chart of tagged pines that were below 50-cm DBH — size class 1 and 2 — and above 50-cm DBH — size class 3, 4, and 5 — before dying. The chart shows the total number of dead pines (N) and their minimum (MinD), median (MedD), and maximum (MaxD) diameter (DBH) before dying. The dotted vertical line highlights the lack of ingrowth records after 1970.
FIGURE II.9. Time-series chart of pine mortality, by size class (1, 2, 3, 4, 5 and TOT, which represents all sizes) and by 10-year interval. Mortality was computed as percentage of density at the beginning of the interval, using all available observations.
FIGURE II.10. Time-series chart of pine mortality as percentage of density at the beginning of the 10-year interval. Mortality was computed using all available observations for pines whose stem diameter before dying was smaller than 50 cm — M(S1–2) — and larger than 50 cm — M(S3–5). It is evident that mortality of large pines was greater and increased more through time than mortality of small pines.
Time-series chart of tagged pines that reached DBH greater than 50 cm during each 10-year interval. The chart shows the total number of such pines (N) and their minimum (MinD), median (MedD), and maximum (MaxD) stem diameter before they exceeded 50-cm DBH.
FIGURE II.12. Time-series chart of pine outgrowth, by size class (1, 2, 3, 4, 5 and TOT, which represents all sizes) and by 10-year interval. Outgrowth was computed as percentage of density at the beginning of the interval, using all available observations.
FIGURE II.13. Time-series chart of mortality and outgrowth as percentage of stand density at the beginning of the 10-year interval. Outgrowth from size class 2 — O1(S2) — and mortality of pines in size class 3, 4, and 5 — M(S3-5) — were computed as percentage of the number of pines in those size classes. Outgrowth from size class 2 was also computed — O2(S2) — as percentage of pines in size class 3, 4, and 5 in order to compare input — O2(S2) — and output — M(S3-5) — of pines above 50-cm DBH.
FIGURE II.14. Time-series chart of total periodic basal area increment (TPBAI) on plots 1–29. All available observations were used to compute plot values.
Inventory Data (1920 Pines, by plot)

FIGURE II.15. Time-series chart of total periodic basal area increment (TPBAI) on plots 1–29. Only observations on pines present in 1920 were used to compute plot values.
Inventory Data (All pines, 1990 DBH < 50 cm)

FIGURE II.16. Time-series chart of total periodic basal area increment (TPBAI) on plots 1–29. Only observations on pines with 1990 DBH smaller than 50 cm were used to compute plot values. Of the 4,221 such pines measured in 1990, a total of 3,088 entered the inventory after 1920.
FIGURE 11.17. Time-series chart of total periodic basal area increment (TPBAI) on plots 1–29. Only observations on the 1,133 pines present in 1920 and smaller than 50-cm DBH in 1990 were used to compute plot values.
FIGURE II.18. Time-series chart of total periodic basal area increment (TPBAI) on plots 1–29. Only observations on pines with 1990 DBH larger than 50 cm were used to compute plot values. Of the 946 such pines measured in 1990, only two entered the inventory after 1920.
FIGURE II.19. Histograms and box plots of 10-year periodic basal area increment (PBAI) computed for three time intervals using all available observations ('ALL PINES' column) and observations on pines first inventoried ('1920 PINES' column). The number of observations (N) is given in each histogram. The x-axis scale is constant for all histograms, the y-axis scale is constant only for histograms in the same column. The 2,077 observations included in the lower-right histogram were taken on pines always present from 1920 to 1990.
Inventory Data (Cored pines, 1990 DBH≥50 cm)

FIGURE II.20. Time-series chart of periodic basal area increment of pines cored on plots 1–29. Only observations on the 29 pines larger than 50-cm DBH in 1990 were used.
Inventory Data (Cored pines, 1990 DBH < 50 cm)

FIGURE II.21. Time-series chart of periodic basal area increment of pines cored on plots 1–29. Only observations on the 29 pines smaller than 50-cm DBH in 1990 were used.
FIGURE II.22. Histogram and box plot (left), together with normal probability plot (right) of residuals from the mixed linear model fitted to periodic basal area increment (PBAI, cm$^2$ $\pi^{-1}$) of pines randomly selected in 1990 (above) and of pines present in 1920 (below). The number of observations (N) in each histogram is given by the number of samples — 58 above and 2,519 below — times the number of time periods — 7 — minus the number of missing values — 34 above and 1,318 below.
FIGURE II.23. Time-series chart of estimated slope parameters for the mixed linear model computed using pines present in 1920. Each parameter represents 'typical' growth rates for a given size class and period. Only the parameter for size class 5 in period 1970–80 was not significantly different from zero (Table 4). Notice how growth rates declined in all size classes, but with different steepness, so that the order of growth rates by size class reversed during the observation interval.
TABLE II.1. Statistics of pines measured at each inventory, by size class.

<table>
<thead>
<tr>
<th>Size Class</th>
<th>Year</th>
<th>N</th>
<th>MinD (cm)</th>
<th>MedD (cm)</th>
<th>MaxD (cm)</th>
<th>CV (%)</th>
<th>TBA (m$^2$π$^{-1}$)</th>
<th>TPBAI (m$^2$π$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1920</td>
<td>1046</td>
<td>7.9</td>
<td>14.7</td>
<td>29.7</td>
<td>34.2</td>
<td>7.7</td>
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</tr>
<tr>
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<td>1920</td>
<td>617</td>
<td>30.0</td>
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<td>49.8</td>
<td>13.7</td>
<td>25.9</td>
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<td>69.9</td>
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</tr>
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<td>4</td>
<td>1920</td>
<td>245</td>
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MinD, MedD, MaxD: Minimum, median and maximum stem diameter (DBH)
CV: Coefficient of variation
TPBAI: Total Periodic Basal Area Increment

TBA: Total Basal Area

(see text for details)
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MinD, MedD, MaxD: Minimum, median and maximum stem diameter (DBH)
CV: Coefficient of variation
TPBAI: Total Periodic Basal Area Increment
TBA: Total Basal Area

(see text for details)
TABLE II.1. (continued).

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<th>Year</th>
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<th>MinD (cm)</th>
<th>MedD (cm)</th>
<th>MaxD (cm)</th>
<th>CV (%)</th>
<th>TBA (m²π⁻¹)</th>
<th>TPBAI (m²π⁻¹)</th>
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MinD, MedD, MaxD: Minimum, median and maximum stem diameter (DBH)

CV: Coefficient of variation

TPBAI: Total Periodic Basal Area Increment

TBA: Total Basal Area

(see text for details)
TABLE II.2. Statistics of pines moving into the next larger size class during a 10-year interval.

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MinD, MedD, MaxD: Minimum, median and maximum stem diameter (DBH)
TABLE II.2. (continued).

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MinD, MedD, MaxD: Minimum, median and maximum stem diameter (DBH)
TABLE II.2. (continued).

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<th>MaxD</th>
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MinD, MedD, MaxD: Minimum, median and maximum stem diameter (DBH)
TABLE II.3. Statistics of periodic basal area increment, measured on pines present in 1920, by size class.

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<th>Size Class</th>
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<th>Med (cm²/yr)</th>
<th>Max (cm²/yr)</th>
<th>CV (%)</th>
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Size Class is defined by stem DBH at the beginning of the period, as in Table 2.

Med, Max: Median and maximum PBAI (minimum PBAI = 0).

CV: Coefficient of variation

TPBAI: Total Periodic Basal Area Increment (see text for details)

TBA: Total Basal Area
TABLE II.3. (continued).

<table>
<thead>
<tr>
<th>10-Year Period</th>
<th>Size Class</th>
<th>N (cm²π⁻¹)</th>
<th>Med (cm²π⁻¹)</th>
<th>Max (cm²π⁻¹)</th>
<th>CV (%)</th>
<th>TPBAI (m²π⁻¹)</th>
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<td>3</td>
<td>648</td>
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<td>136.8</td>
<td>67.6</td>
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<tr>
<td></td>
<td>4</td>
<td>274</td>
<td>31.0</td>
<td>119.7</td>
<td>78.8</td>
<td>1.0</td>
</tr>
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<td>5</td>
<td>43</td>
<td>38.0</td>
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</tbody>
</table>

Size Class is defined by stem DBH at the beginning of the period, as in Table 2.

Med, Max: Median and maximum PBAI (minimum PBAI = 0).

CV: Coefficient of variation
TPBAI: Total Periodic Basal Area Increment
TBA: Total Basal Area

(see text for details)
TABLE II.3. (continued).

<table>
<thead>
<tr>
<th>10-Year Period</th>
<th>Size Class</th>
<th>N</th>
<th>Med (cm$^2 \pi^{-1}$)</th>
<th>Max (cm$^2 \pi^{-1}$)</th>
<th>CV (%)</th>
<th>TPBAI (m$^2 \pi^{-1}$)</th>
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</thead>
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<td>2</td>
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<td>107.0</td>
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<td>3</td>
<td>620</td>
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<td>2.0</td>
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</table>

Size Class is defined by stem DBH at the beginning of the period, as in Table 2.

Med, Max: Median and maximum PBAI (minimum PBAI = 0).

CV: Coefficient of variation

TPBAI: Total Periodic Basal Area Increment

TBA: Total Basal Area

(see text for details)
TABLE II.4. Statistics of fixed effects included in the mixed linear model computed using pines present in 1920.

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<tr>
<th>Size Class</th>
<th>Period</th>
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<th>S.E.</th>
<th>DF</th>
<th>T</th>
<th>Pr &gt;</th>
<th>t</th>
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S.E.: Standard error of estimate.  DF: Degrees of freedom.
T: t-statistic for the estimate  Pr > |t|: p-value for a two-sided t-test.
TABLE II.4. (continued)

| Size Class | Period   | Estimate | S.E. | DF   | T    | Pr > |T| |
|------------|----------|----------|------|------|------|------|----|
| 4          | 1920–30  | 61.7     | 1.31 | 16280| 47.23| < 0.001|
| 4          | 1930–40  | 49.2     | 1.20 | 16280| 41.00| < 0.001|
| 4          | 1940–50  | 29.7     | 1.14 | 16280| 26.03| < 0.001|
| 4          | 1950–60  | 28.4     | 1.12 | 16280| 25.32| < 0.001|
| 4          | 1960–70  | 23.1     | 1.11 | 16280| 20.75| < 0.001|
| 4          | 1970–80  | 9.1      | 1.16 | 16280| 7.85 | < 0.001|
| 4          | 1980–90  | 16.7     | 1.21 | 16280| 13.75| < 0.001|
| 5          | 1920–30  | 59.2     | 3.34 | 16280| 17.71| < 0.001|
| 5          | 1930–40  | 43.3     | 2.98 | 16280| 14.52| < 0.001|
| 5          | 1940–50  | 28.7     | 2.80 | 16280| 10.28| < 0.001|
| 5          | 1950–60  | 23.6     | 2.70 | 16280| 8.76 | < 0.001|
| 5          | 1960–70  | 19.1     | 2.74 | 16280| 6.94 | < 0.001|
| 5          | 1979–80  | −1.7     | 3.03 | 16280| −0.57| 0.566|
| 5          | 1980–90  | 12.4     | 3.21 | 16280| 3.87 | < 0.001|

S.E.: Standard error of estimate.  DF: Degrees of freedom.
T: t-statistic for the estimate  Pr > |T|: p-value for a two-sided t-test.
III. SPATIO-TEMPORAL PATTERNS OF STEM SIZE AND INCREMENT

III.1. Introduction

Estimation and mapping of forest resources is a fundamental necessity of land management, planning and research. Time and cost constraints do not usually allow exhaustive measurements, hence sampling schemes need to be designed and implemented to estimate population values (Husch et al. 1982). Foresters deal with spatially distributed samples and variables, and they have long been aware that spatial correlation contradicts common statistical assumptions, e.g. independence of observations (Matérn 1960, Clutter et al. 1983). Analyses of forest structure and dynamics that incorporate, rather than exclude, information on spatial variability provide a more accurate description of reality. Moreover, estimating the amount of variation due to spatial dependence at different scales provides a basis for designing effective experiments (Jeffers 1982). Mapping often requires interpolation of available data to estimate values at unsampled locations and compute spatial averages. Of all interpolation techniques currently used, kriging is the best linear unbiased estimator. Kriging allows declustering of data points and it provides an estimate of mapping error. Most importantly, kriging incorporates information on spatial dependence, or continuity, of the variable being mapped, and is fully supported by regionalized variable theory, also known as geostatistics (Matheron 1963, 1965).

Regionalized variables are assumed to be spatially correlated to one another over
short distances, but independent of one another over large distances (Isaaks and Srivastava 1989, Cressie 1991). This assumption has proven both flexible and powerful for answering research and management questions in the spatial domain. After its original use in ore exploration and mining (Krige 1966), geostatistics has been applied in a number of disciplines including geology (Olea 1977), soil science (Burgess and Webster 1980a, 1980b), remote sensing (Carr and Myers 1984), pollution studies (Lefohn et al. 1987), ecology (Robertson 1987), phytopathology (Lecoultre et al. 1989), geography (Oliver et al. 1989a, 1989b), hydrology (ASCE 1990a, 1990b), entomology (Liebhold et al. 1991), climatology (Bigg 1991) and meteorology (Hevesi et al. 1992a, 1992b). Rossi et al. (1992) provide an extensive review of geostatistical models to interpret spatial dependence in ecological studies.

The potential of regionalized variable theory for forestry applications has not yet been fully exploited. Matérn (1960) supplied a rigorous and extensive treatment of the theory, and used correlograms to examine problems in forest sampling. Samra et al. (1989) used variograms to analyze spatial heterogeneity of tree height after one, two and three years of growth in a Melia azedarach L. plantation. Cohen et al. (1990) analyzed conifer canopy structure by computing variograms from digitized aerial video images. Current research efforts on linking point processes to watershed and landscape processes include GIS (geographical information system) models (Band et al. 1991, Baker 1992), but have not yet employed geostatistical representations of forest structure. Mandallaz (1993) discussed geostatistical estimation methods to merge airborne observations and
ground-truth measurements in forest inventories.

The space available for a tree to grow is determined by its position with respect to nearby trees (Weiner 1988). For instance, intra-species competition for resources reduces growth rates of dominant ponderosa pines (Biondi et al. 1992) and makes them less responsive to environmental variations (Sutherland et al. 1991). The objective of this chapter was to answer the question: does increased stand density simply reduce growth rates or does it also alter spatial interactions among trees? I used geostatistics to test for spatial trends, directional patterns and temporal modifications of spatial dependence. Spatial stochastic models were fitted to measurements of tree size and increment at 10-year intervals, from 1920 to 1990. The study area was a naturally-seeded, old-growth forest undergoing endogenous modification of its horizontal and vertical structure (Chapter II).

III.2. Materials and Methods

III.2.1. Geostatistical background

Geostatistical methods are based on a fundamental assumption: if a variable is observed at several spatial locations, its estimate at any unsampled location should be most dependent on the nearest observations. In other words, the correlation between observations for pairs of locations decreases with increasing distance between the
locations. Dependence on nearby data locations and estimation uncertainty are expressed mathematically by a random function model (Myers 1991). Let $Z(x)$ denote the regionalized variable $Z$ at location $x$, $x$ being a point in two- or three-dimensional space. Each $Z(x)$ is a random variable, and the collection of such random variables — for every $x$ in a region of interest — is a random function. The spatial dependence of these random variables is considered a function of the separation vector. Mathematically, the assumptions imposed on $Z(x)$ are as follows (Myers 1991):

$$E \left[ Z(x+d) - Z(x) \right] = 0 \quad \text{for every } x \text{ and } d$$

$$0.5 \ V \left[ Z(x+d) - Z(x) \right] = \gamma(d) \quad \text{exists and depends only on } d$$

where $E$ denotes expectation, $d$ is the separation vector, $V$ means variance, and $\gamma(d)$ is the variogram of $Z(x)$. If $\gamma(d)$ depends on the length of $d$ but not on its direction, then $Z(x)$ and $\gamma(d)$ are said to be isotropic. A spatial trend, or drift, exists when the probability laws that control the random function depend on spatial location (Isaaks and Srivastava 1989). The use of random function models for interpolating spatial data was introduced by Matérn (1960) and Matheron (1963, 1965). Matérn referenced the variogram, but used the covariance function and the correlogram, graphical representations of, respectively, the spatial (auto)covariance and (auto)correlation. Matheron placed much more emphasis on the variogram, which is based on weaker stationarity assumptions (Myers 1989). The variogram is easier to estimate than the covariance function or the correlogram because it does not require quantifying the mean of $Z(x)$.

To clarify, $Z(x)$ is a "model" for the variable of interest, and $\gamma(d)$ is a "parameter"
of the model. In general $\gamma (d)$ is not known \textit{a priori} and must be estimated from the data. The sample variogram is the simplest estimator of $\gamma (d)$ (Isaaks and Srivastava 1988, Myers 1991). The sample variogram is computed after sorting all possible pairs of locations into classes by distance and direction. The sample variogram value for a certain distance and direction is the sum of squared differences between all pairs of observations $(x_i, x_k)$ that belong to the distance class $r$ and angle window $\theta$, as follows:

$$\gamma (r, \theta) = \frac{0.5}{N(r, \theta)} \sum_{i,k} [Z(x_i) - Z(x_k)]^2$$

Directional sample variograms are usually computed for $\theta$ equal to 0, 45, 90 and 135° with an angle tolerance of ±22.5°. The omnidirectional sample variogram is computed for $\theta$ equal to 0° with an angle tolerance of ±90°. Sample variograms are then plotted against distance to check for directional dependence (anisotropy) and to choose a model for the variogram. Variogram models are needed to solve the ordinary kriging equations, hence they must satisfy a form of positive definiteness. Valid variogram models include the nugget, spherical, exponential, Gaussian and linear model; positive linear combinations of these models may be used. The distance at which the variogram model reaches a constant value is called the \textit{range}, and the constant value is called the \textit{sill}. The Gaussian and exponential models reach the sill asymptotically, hence their range is defined as the distance at which the variogram value is 95% of the sill. The linear model does not have a range and sill, but their ratio is the slope of the line. The nugget model corresponds
to no spatial dependence, i.e. pure randomness (Isaaks and Srivastava 1989).

The ordinary kriging estimator of a regionalized variable at any unsampled location is a weighted sum of values at nearby locations. The form of the estimator is the same for estimates at a single point — point kriging — or for estimates of the average value over an area — block kriging. The kriging weights are a function of the unsampled location and are determined by imposing two conditions on the estimator: (a) unbiasedness, and (b) minimum variance of the estimation error. While all sampled locations could be used to produce all estimates, it is customary to specify a search neighborhood that identifies the data locations closest to the unsampled location. Kriging variance, i.e. the minimized variance of the estimation error, can be computed using kriging weights and represents a relative ranking of model reliability. The availability of public domain software (Englund and Sparks 1989) makes geostatistical tools easily accessible and inexpensive.

III.2.2. Field measurements and data analysis

Subplot corners at the Gus Pearson Natural Area were accurately mapped in 1991 by two registered surveyors using an Electromagnetic Distance Measuring (EDM) system (Whyte and Paul 1985). The subplot corners were then used as reference points to map all the tagged ponderosa pines included in a 100x400-m, north-to-south area formed by subplots 5, 12, 13 and 20. Stem coordinates were first obtained as polar coordinates
using a staff compass and a measuring tape. Polar coordinates were converted into x-y coordinates using as reference point the south-west corner of the area. Subplots were simply a grid of smaller land units that did not differ in terms of vegetation forming factors (Major 1951). Hence, the four mapped subplots were merged in the final analysis. Stem maps were checked in the field for possible errors and were found accurate, on average, to the nearest meter. Maximum inter-tree distance was 410.5 m among a total of 183,921 pairs.

The spatial dependence of stem size and increment was analyzed using variograms and ordinary block kriging. Stem DBH, BA, and BAI were studied at 10-year intervals, from 1920 to 1990. To model spatial dependence at multiple scales, sample variograms were computed for (a) 1-m lags up to a maximum distance of 24 m, (b) 2.5-m lags up to a maximum of 60 m, and (c) 4-m lags up to 96 m. Each sample variogram was computed twice, first using all available trees — the general sample, with N ranging from 424 in 1920 to 605 in 1960 — and second using only trees always present from 1920 to 1990 and with DBH larger than 15.2 cm in 1920 — a restricted sample, with N = 308. The restricted sample was independent of ingrowth records, and it excluded thickets of small pines from the analysis. By comparing results obtained using the general and the restricted sample, it was possible to evaluate the influence of ingrowth, i.e. increased number of small pines, on spatial dependence of stem size and increment. Ordinary block kriging was used to estimate average values over 5x5-m blocks. The search neighborhood allowed a maximum of 20 and a minimum of 3 nearest data points within a circular
search area with maximum search radius of 30 m (Englund and Sparks 1989).

Spatial and temporal variability were analyzed separately. Since data were both spatially and temporally distributed, it might seem that modeling space-time trends jointly would be more appropriate. As pointed out in Rouhani and Myers (1990), there are fundamental differences between spatial dependence and temporal dependence that hamper modeling the joint correlation structure. Because of the lack of a distance measure in space-time, it is usually necessary to treat either the spatially dependent variable separately at each time or the temporally dependent variable separately at each location. In the case of this data set, with many spatial locations but relatively few time points, it was more reasonable to focus on the spatial variability at each time point. The parameters of spatial variability were estimated at each time using a non-random sample from a single realization of the spatially dependent variable. Knowledge of the parameter distribution required assumptions that could not be statistically tested from the data. The nonparametric, univariate Mann-Kendall test (Kendall and Gibbons 1990) was used to evaluate monotone temporal trends of model parameters. Assessing temporal dependence in geostatistical parameters by means of the Mann-Kendall test provided a numerical value for visually persistent tendencies with respect to time.

III.3. Results and Discussion

Stand density increased from 1920 to 1990 (Figure 1). Estimates of stem size and
increment based on all available observations were affected by ingrowth records. Influx of small pines increased the number of observations and decreased median tree size from 1920 to 1950 (Tables 1 and 2). Mortality and lack of ingrowth records lowered the number of observations and raised the average tree size from 1960 to 1990 (Tables 1 and 2). The Mann-Kendall test for N, mean and median of DBH and BA from 1920 to 1990 was not highly significant, having p-values greater than 0.034. Temporal trends in stem size were not affected by ingrowth when described by stem diameter (Table 1) and basal area (Table 2) of trees always present and with DBH greater than 15.2 cm in 1920 — the restricted sample, with N = 308 at all times. Average size of the restricted sample constantly increased from 1920 to 1990: the Mann-Kendall test for mean and median of DBH and BA was equal to 1.00, significant at the 0.0005 level. Size variability of the restricted sample steadily decreased: the Mann-Kendall test for the coefficient of variation of DBH and BA was -0.98 and -1.00 (p-values < 0.001), respectively.

Stem size distributions were analyzed using histograms and box plots (Tukey 1977; Figures 2–5). Results based on the four mapped plots, which included 14% of the study area and from 12 to 17% of all measured pines, were consistent with results obtained for the entire study area (Chapter II). Although minimum tree size increased between 1920 and 1990 — the Mann-Kendall test had p-values ≤ 0.002 —, the histogram shape for DBH remained both bimodal and skewed to right when based on all available observations (Figure 2). Ingrowth of small pines in the 1930–1960 inventories contributed to maintaining skewness of size distributions. When based on the restricted
sample, the histogram shape for DBH gradually changed through time (Figure 3). It was bimodal and skewed to right in 1920 because of a large number of small pines. It became more symmetric, albeit slightly bimodal, in 1990 because diameter increment was greater in smaller trees, thus producing faster outgrowth from the smallest size classes. The bimodal feature of the DBH histogram in 1920 (Figures 2 and 3) was caused by a large number of pines with DBH from 10 to 20 cm. This peak in size frequency was discussed in Chapter II. Histogram shapes for basal area (Figures 4 and 5) were unimodal, but showed changes in skewness that were consistent with those observed for DBH.

Spatial dependence explained a large amount of stem size variability. The directional and omnidirectional sample variograms did not show evidence of spatial trend or anisotropy (Isaaks and Srivastava 1989). At all times from 1920 to 1990, a Gaussian model plus nugget fitted the omnidirectional sample variograms for DBH (Figures 2 and 3) and BA (Figures 4 and 5). In all cases, the model closely matched the sample variograms computed using either 1.0-m, 2.5-m or 4.0-m distance classes. For brevity, only the figures of sample variograms computed using 2.5-m classes were included in this chapter. The variogram model was defined as follows:

$$
\gamma(d) = \begin{cases} 
C_0 + C_1 [1 - \exp(-3d^2a^{-2})] & \text{if } d > 0 \\
0 & \text{if } d = 0 
\end{cases}
$$

where \( \gamma(d) \) is the variogram value for the inter-tree distance \( d \), \( C_0 \) is the nugget, \( C_1 \) is the sill of the Gaussian component, \( C_0 + C_1 \) is the total sill and \( a \) is the range of the
variogram (Figure 2). The Gaussian model is usually best suited for "extremely continuous phenomena" (Isaaks and Srivastava 1989, p. 375). In fact, pines located less than 5–10 m from one another had size extremely similar to one another. The parabolic behavior near the origin and the presence of an inflection point are unique to the Gaussian model. Using 1-m lags to increase resolution at short distances, it was possible to notice a stronger parabolic behavior near the origin, produced by the variogram reaching a minimum after 3–5 m, and increasing at longer as well as shorter distances.

For modeling and simulation purposes, it was remarkable how well the same variogram model could represent spatial dependence of stem size, either diameter (DBH) or basal area (BA), at different spatial scales and at different points in time. Overall, variogram models were affected marginally by ingrowth records, and only in terms of nugget and sill estimates, not of model type or range. The range of variograms for DBH and BA was always 30 m (Tables 1 and 2, Figs 2–5). Ordinary kriging estimates of average basal area over 5x5-m blocks (Figure 6) showed clearly the horizontal patchiness of the stand, caused by a mixture of pine groups. Each group is roughly even-sized, i.e. formed by trees with similar size, but nearby groups are uneven-sized. The variogram range measured the average dimension of these pine groups. Although pine density increased through time, the average dimension of a pine group remained the same, being about 30 m in 1990 as it was in 1920. The consistency through time of variogram models for DBH and BA, with or without ingrowth records, provided strong evidence that size distributions maintained basically the same spatial patterns from 1920 to 1990. Tree
density increased by increasing the number of pine groups, not their horizontal dimension.

The nugget, $C_0$, of variogram models quantifies spatial variability at near-zero distances, whereas the sill of the Gaussian model component, $C_1$, quantifies spatial variability at distances greater than those covered by spatial dependence. In variogram models of stem size, the nugget was always much less than the sill of the Gaussian component (Tables 1 and 2, Figures 2–5). All variogram models had a finite sill, hence it was possible to compute the percentage of spatial variance explained by spatial dependence. This percentage was computed from the ratio $C_1/(C_0 + C_1)$ and provided a relative value of spatial dependence, useful for making comparisons. Spatial dependence ($S$) of stem diameter ranged from 68–78 to 82–92%, slightly less than spatial dependence of stem basal area, ranging from 74–81 to 85–93% (Tables 1 and 2). Whenever such a large spatial dependence exists, point and area estimates of tree size greatly benefit by including information on horizontal stand structure, especially tree location and inter-tree distance.

Spatial dependence of stem size gradually decreased from 1920 to 1990 (Tables 1 and 2). The Mann-Kendall test for spatial dependence ($S$) of DBH and BA ranged from -0.94 (p-value = 0.002) to -1 (p-value < 0.001). The time-related decrease in spatial dependence of stem size was mostly an effect of increasing nugget — p-values ≤ 0.004 for the Mann-Kendall test — and of decreasing sill — the Mann-Kendall test for $C_1$ of DBH was equal to -1.00, p-value < 0.001. Small ponderosa pines form dense groups, or thickets, where many inter-tree distances are less than 2.5 m, the distance lag used in Figs
An increase in the number of small pines corresponded to an increased number of the smallest inter-tree distances, which presumably increased the nugget term of variogram models. The increase in spatial variability at near-zero distances with clustering of trees had already generated the parabolic behavior observed in sample variograms computed for 1.0-m distance classes.

Temporal patterns of stem growth rates (Table 3) were consistent when estimated using observations on all available pines (Figure 7) and observations on a constant number of pines (Figure 8). Individual growth rates decreased over time: the Mann-Kendall test for mean and median BAI was -0.81, p-value = 0.011. In the last decade, 1980–90, mean and median BAI of the restricted sample were less than half of those in the first decade, 1920–30 (Table 3). Variance of 10-year periodic basal area increment also decreased over time — the Mann-Kendall test was -0.90, p-value = 0.004. Mean BAI decreased more through time than its variance, hence the coefficient of variation for BAI increased over time — p-value ≤ 0.024. This was reflected by increased asymmetry of the data distribution from 1920 to 1990 (Figures 7 and 8). As shown by BAI histograms based on trees always present (Figure 8), skewness to the right became stronger as growth rates of more and more pines became smaller. The same pattern appeared in BAI histograms based on all available trees (Figure 7) even though new, small pines kept entering the inventories from 1930 to 1970 (Figures 1–3, Table 1). Therefore, the reduction of individual growth rates over time was tied to increased pine density, which usually intensifies intra-species competition for resources (Biondi et al.
Kriged estimates of average basal area increment over 5x5-m blocks (Figure 9) showed that reduction of growth rates from 1920–30 to 1980–90 was not spatially clustered and was common to the entire stand.

The directional and omnidirectional sample variograms of BAI showed no evidence of spatial trend or anisotropy. A nugget plus Gaussian variogram model adequately described spatial dependence of stem increment at all times and distance lags (Figures 7 and 8). Competitive interactions in southwestern ponderosa pine forests concentrate belowground (Cooper 1960, 1961) and are usually symmetric, i.e. small trees compete with large trees (Biondi et al. 1992). Presumably, the isotropic structure of root systems in ponderosa pine and the flat terrain favored isotropic competitive interactions, resulting in isotropic spatial dependence of growth rates. The range of variogram models for BAI was always 30 m, but even shorter ranges could be considered, partly because of the limited amount of spatial dependence. Considering that spatial variation of growth rates was being modeled, the variogram range could be used to represent the maximum distance spanned by inter-tree competitive interactions. Therefore, average competitive radius did not exceed average patch size. The absence of spatial dependence beyond 30-m distances suggests a lack of spatial variation in soil properties, which were found to be responsible for spatial dependence in tree growth at scales larger than any reasonable competitive radius (Samra et al. 1989).

Spatial dependence of stem increment was smaller and decreased more through time than that of stem size (Table 3, Figures 7 and 8). Spatial dependence of BAI was
31–47% in 1920 and 2–19% in 1990. Omnidirectional sample variograms for BAI "flattened out", *i.e.* showed a decrease in spatial dependence after 1950. The nugget component of variogram models for BAI was always greater than the sill of the Gaussian component (Table 3). This indicated that growth variation at short distances was not much different from growth variation at long distances. The variogram model for the 1980–90 period was almost a pure nugget model, since the Gaussian component was quasi non-existent (Figures 7 and 8). A pure nugget variogram model entails a complete lack of spatial dependence, *i.e.* "the data value at any particular location bears no similarity even to very nearby data values" (Isaaks and Srivastava 1989, p. 307). In these situations, knowledge of sample location does not improve estimation of point values or area averages. In other words, prediction of stem increment becomes independent of mutual tree position.

The geostatistical models of stem growth rates described here could be explained by the increased stand density during the twentieth century. Crowding not only reduced average basal area increments, but it also altered spatial dependence of growth rates. At low densities, resources available to a tree are mostly a function of the tree position with respect to surrounding trees. At high densities, resources available to a tree become more dependent on the ability of the tree to compete, based on the tree’s sociological status, genetic potential, and microsite — *e.g.* within or on the edge of a patch. Separating effects of competition, tree vigor, microsite, etc. on growth variation was not the objective of this study. However, reduced spatial dependence of BAI with increasing stand density
strongly suggests that growth variation is a function of inter-tree distance only when local crowding does not exceed threshold values. Since crowding reduced the dependence of individual tree growth on mutual tree position, prediction of growth rates for any given tree cannot rely on inter-tree distances alone. Further research should estimate the time needed for a modification in spatial dependence of growth rate to affect spatial patterns of tree size.

III.4. Conclusions

Modeling spatial dependence helped to characterize site occupation in old-growth ponderosa pine forests. In the last century, the structure of ponderosa pine stands in the American Southwest has changed from an open forest with scattered large trees to a more closed forest where the gaps between and around large trees have been occupied by thickets of small trees. In this study, spatial dependence of tree size and increment was mostly related to stand density because climate, topography, geology, soil and vegetation type, disturbance history and anthropic manipulation were homogeneous over the study area. Stem size behaved as a regionalized variable; it was spatially autocorrelated over distances up to 30 m. The consistency through time of variogram models used to represent spatial dependence of DBH and BA provided strong evidence that tree size distributions maintained basically the same spatial patterns from 1920 to 1990. Tree density increased by adding new pine groups rather than by enlarging the horizontal
dimension of existing groups.

This result agrees with previous studies of ponderosa pine forest structure in the Southwest. Cooper (1960) found that size of pine groups in the White Mountains of eastern Arizona ranged from 0.16 to 0.32 acre, equivalent to an horizontal distance of 28–40 m. The size of pine groups identified by White (1985) on a 7.3-ha tract of the Gus Pearson Natural Area ranged from 0.02 to 0.29 ha, equivalent to horizontal distances of 16–60 m. The median size of White’s (1985) groups was 0.07 ha, equivalent to an horizontal distance of 30 m. Moore et al. (1993), working in the Flagstaff area, obtained an average group size of 0.16 acre, with a range of 0.08 to 0.64 acre, equivalent to an average horizontal distance of 29 m and a range of 20 to 57 m. According to Oliver and Ryker (1990), most seedfall in ponderosa pine forests occurs within 30–40 m from the seed source. Regeneration and ingrowth at the study area continued during the twentieth century without the interference of fire (Chapter II). Hence, natural dissemination patterns may be responsible for the size of pine groups.

Variogram models indicated that spatial dependence from 1920 to 1990 decreased more for stem increment than for stem size. Increased tree density was associated with decreased mean and variance of individual tree growth, as well as with reduced spatial dependence of stem size and increment. In particular, basal area increment from 1980 to 1990 showed almost no spatial dependence, indicating that trees grew at different rates regardless of their proximity. Since growth variation was less affected by inter-tree distance with greater local crowding, prediction of individual growth rates cannot rely on
inter-tree distances alone. Presumably, increased tree density intensified competitive interactions, which in turn disrupted spatial patterns of stem increment. In other words, these results indicate that density-dependent limitation of tree growth does not necessarily generate distance-dependent growth rates. For simulation purposes, it was remarkable how well the same variogram model could represent spatial dependence of stem size at different spatial scales and over different time periods. The Gaussian model, which portrayed spatial dependence of stem diameter and basal area over a large range of stand densities, was both empirically and theoretically meaningful. Although the features that distinguish spatio-temporal patterns of this old-growth ponderosa pine forest need to be examined elsewhere to determine their generality, finding other extensive permanent plots that have been maintained since AD 1920 in pristine forest may not be simple.
Map of pines included in the first (1920, N = 424) and last (1990; N = 590) forest inventory of plots 5, 12, 13 and 20. Circle diameter is proportional to stem DBH and is on a different scale than stem coordinates. Location of pines included in all forest inventories (1920–1990, N = 308) is also shown; circle diameter is proportional to stem DBH in 1990.
FIGURE III.2. Histogram, box plot, and omnidirectional sample variogram for stem diameter (DBH) of pines included in the 1920 (N = 424), 1950 (N = 567), and 1990 (N = 590) forest inventory. The Gaussian variogram model for 1920 includes a graphical representation of its nugget ($C_0$), range ($a$), and total sill ($C_0 + 0.95 C_1$).
FIGURE III.3. Histogram, box plot, and omnidirectional sample variogram for stem diameter (DBH) of pines always present in the 1920–90 inventories (N = 308).
FIGURE III.4. Histogram, box plot, and omnidirectional sample variogram for stem basal area (BA) of pines included in the 1920 (N = 424), 1950 (N = 567), and 1990 (N = 590) forest inventory.
FIGURE III.5. Histogram, box plot, and omnidirectional sample variogram for stem basal area (BA) of pines always present in the 1920–90 inventories (N = 308).
FIGURE III.6. Ordinary kriging estimates, on 5x5-m blocks, of stem basal area in 1920 and in 1990, based on pines always present (N = 308).
FIGURE III.7. Histogram, box plot, and omnidirectional sample variogram for 10-year basal area increment (BAI) of pines included in the 1920–30 (N = 424), 1950–60 (N = 567), and 1980–90 (N = 589) forest inventories.
Histogram, box plot, and omnidirectional sample variogram for 10-year basal area increment (BAI) of pines always present in the 1920–90 inventories (N = 308).
Ordinary kriging estimates, on 5x5-m blocks, of 10-year basal area increment in 1920–30 and in 1980–90, based on pines always present (N = 308).
### TABLE III.1. Statistics of stem diameter (DBH, cm).

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<th>Year</th>
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<th>Var</th>
<th>CV (%)</th>
<th>Min</th>
<th>Med</th>
<th>Max</th>
<th>a (m)</th>
<th>C₀</th>
<th>C₁</th>
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Estimates based on the same trees for each year

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<th>CV (%)</th>
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<th>Med</th>
<th>Max</th>
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<th>C₀</th>
<th>C₁</th>
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<td>100</td>
<td>215</td>
<td>68</td>
</tr>
</tbody>
</table>

CV: Coefficient of variation

a: Range of sample variogram

C₀: Nugget of sample variogram

C₁: Sill of sample variogram

S: Spatial dependence, given by the ratio 100 C₁ / (C₀ + C₁).
TABLE III.2. Statistics of stem basal area (BA, cm$^2 \pi^{-1}$).

<table>
<thead>
<tr>
<th>Year</th>
<th>N</th>
<th>Mean</th>
<th>Var</th>
<th>CV (%)</th>
<th>Min</th>
<th>Med</th>
<th>Max</th>
<th>a (m)</th>
<th>$C_0$ x10$^3$</th>
<th>$C_1$ x10$^3$</th>
<th>S (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1920</td>
<td>424</td>
<td>445.5</td>
<td>202432</td>
<td>101</td>
<td>15.6</td>
<td>347.8</td>
<td>1962.5</td>
<td>30</td>
<td>16</td>
<td>220</td>
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<td>211691</td>
<td>105</td>
<td>20.7</td>
<td>243.4</td>
<td>2088.5</td>
<td>30</td>
<td>23</td>
<td>220</td>
<td>91</td>
</tr>
<tr>
<td>1940</td>
<td>505</td>
<td>451.4</td>
<td>218961</td>
<td>104</td>
<td>22.1</td>
<td>232.6</td>
<td>2209.0</td>
<td>30</td>
<td>30</td>
<td>210</td>
<td>88</td>
</tr>
<tr>
<td>1950</td>
<td>567</td>
<td>431.6</td>
<td>221310</td>
<td>109</td>
<td>20.7</td>
<td>213.2</td>
<td>2294.4</td>
<td>30</td>
<td>40</td>
<td>200</td>
<td>83</td>
</tr>
<tr>
<td>1960</td>
<td>605</td>
<td>435.5</td>
<td>223653</td>
<td>109</td>
<td>27.0</td>
<td>220.5</td>
<td>2376.6</td>
<td>30</td>
<td>45</td>
<td>200</td>
<td>82</td>
</tr>
<tr>
<td>1970</td>
<td>605</td>
<td>461.4</td>
<td>229368</td>
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<td>52.6</td>
<td>243.4</td>
<td>2490.0</td>
<td>30</td>
<td>45</td>
<td>205</td>
<td>82</td>
</tr>
<tr>
<td>1980</td>
<td>594</td>
<td>472.4</td>
<td>226256</td>
<td>101</td>
<td>57.8</td>
<td>256.0</td>
<td>2540.2</td>
<td>30</td>
<td>45</td>
<td>200</td>
<td>82</td>
</tr>
<tr>
<td>1990</td>
<td>590</td>
<td>493.1</td>
<td>225753</td>
<td>96</td>
<td>60.1</td>
<td>283.1</td>
<td>2621.4</td>
<td>30</td>
<td>45</td>
<td>195</td>
<td>81</td>
</tr>
</tbody>
</table>

Estimates based on all available trees for each year.

<table>
<thead>
<tr>
<th>Year</th>
<th>N</th>
<th>Mean</th>
<th>Var</th>
<th>CV (%)</th>
<th>Min</th>
<th>Med</th>
<th>Max</th>
<th>a (m)</th>
<th>$C_0$ x10$^3$</th>
<th>$C_1$ x10$^3$</th>
<th>S (%)</th>
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<tbody>
<tr>
<td>1920</td>
<td>308</td>
<td>561.7</td>
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<td>78</td>
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<td>470.9</td>
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<td>33</td>
<td>185</td>
<td>85</td>
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<tr>
<td>1930</td>
<td>308</td>
<td>611.8</td>
<td>202598</td>
<td>74</td>
<td>68.1</td>
<td>522.1</td>
<td>2088.5</td>
<td>30</td>
<td>40</td>
<td>190</td>
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<td>308</td>
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<td>76.6</td>
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<td>81</td>
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<td>68</td>
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<td>604.0</td>
<td>2294.4</td>
<td>30</td>
<td>50</td>
<td>195</td>
<td>80</td>
</tr>
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<td>1960</td>
<td>308</td>
<td>724.9</td>
<td>221678</td>
<td>65</td>
<td>91.2</td>
<td>645.2</td>
<td>2376.6</td>
<td>30</td>
<td>55</td>
<td>195</td>
<td>78</td>
</tr>
<tr>
<td>1970</td>
<td>308</td>
<td>754.6</td>
<td>228204</td>
<td>63</td>
<td>93.1</td>
<td>681.2</td>
<td>2490.0</td>
<td>30</td>
<td>60</td>
<td>198</td>
<td>77</td>
</tr>
<tr>
<td>1980</td>
<td>308</td>
<td>772.2</td>
<td>229681</td>
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<td>195</td>
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<tr>
<td>1990</td>
<td>308</td>
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<td>233927</td>
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<td>93.1</td>
<td>727.7</td>
<td>2621.4</td>
<td>30</td>
<td>70</td>
<td>195</td>
<td>74</td>
</tr>
</tbody>
</table>

CV: Coefficient of variation

$C_0$: Nugget of sample variogram

$C_1$: Sill of sample variogram

S: Spatial dependence, given by the ratio $100 C_1 / (C_0 + C_1)$. 

a: Range of sample variogram
TABLE III.3. Statistics for 10-year basal area increment (BAI, cm² π⁻¹)

<table>
<thead>
<tr>
<th>Year</th>
<th>N</th>
<th>Mean</th>
<th>Var (cm²)</th>
<th>CV (%)</th>
<th>Min</th>
<th>Med</th>
<th>Max (m)</th>
<th>a (m)</th>
<th>C₀</th>
<th>C₁</th>
<th>S (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1920–30</td>
<td>424</td>
<td>43.8</td>
<td>787.0</td>
<td>64</td>
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<td>39.0</td>
<td>181.3</td>
<td>30</td>
<td>410</td>
<td>370</td>
<td>47</td>
</tr>
<tr>
<td>1930–40</td>
<td>479</td>
<td>37.4</td>
<td>586.3</td>
<td>65</td>
<td>0</td>
<td>33.0</td>
<td>177.8</td>
<td>30</td>
<td>350</td>
<td>230</td>
<td>40</td>
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<tr>
<td>1940–50</td>
<td>505</td>
<td>29.6</td>
<td>467.6</td>
<td>73</td>
<td>0</td>
<td>24.4</td>
<td>142.2</td>
<td>30</td>
<td>280</td>
<td>180</td>
<td>39</td>
</tr>
<tr>
<td>1950–60</td>
<td>567</td>
<td>30.3</td>
<td>411.9</td>
<td>67</td>
<td>0</td>
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<td>125.4</td>
<td>30</td>
<td>300</td>
<td>120</td>
<td>29</td>
</tr>
<tr>
<td>1960–70</td>
<td>605</td>
<td>25.9</td>
<td>351.4</td>
<td>72</td>
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<td>220</td>
<td>120</td>
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<td>1970–80</td>
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<td>82.6</td>
<td>30</td>
<td>160</td>
<td>50</td>
<td>24</td>
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<tr>
<td>1980–90</td>
<td>589</td>
<td>23.7</td>
<td>306.3</td>
<td>74</td>
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<td>21.8</td>
<td>115.5</td>
<td>30</td>
<td>260</td>
<td>60</td>
<td>19</td>
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</tbody>
</table>

Estimates based on the same trees for each year

<table>
<thead>
<tr>
<th>Year</th>
<th>N</th>
<th>Mean</th>
<th>Var (cm²)</th>
<th>CV (%)</th>
<th>Min</th>
<th>Med</th>
<th>Max (m)</th>
<th>a (m)</th>
<th>C₀</th>
<th>C₁</th>
<th>S (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1920–30</td>
<td>308</td>
<td>50.1</td>
<td>806.0</td>
<td>57</td>
<td>0</td>
<td>45.3</td>
<td>181.3</td>
<td>30</td>
<td>530</td>
<td>240</td>
<td>31</td>
</tr>
<tr>
<td>1930–40</td>
<td>308</td>
<td>43.2</td>
<td>648.0</td>
<td>59</td>
<td>0</td>
<td>39.0</td>
<td>177.8</td>
<td>30</td>
<td>410</td>
<td>220</td>
<td>35</td>
</tr>
<tr>
<td>1940–50</td>
<td>308</td>
<td>34.5</td>
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<td>69</td>
<td>0</td>
<td>31.1</td>
<td>142.2</td>
<td>30</td>
<td>400</td>
<td>170</td>
<td>30</td>
</tr>
<tr>
<td>1950–60</td>
<td>308</td>
<td>35.4</td>
<td>507.5</td>
<td>64</td>
<td>0</td>
<td>31.4</td>
<td>125.4</td>
<td>30</td>
<td>400</td>
<td>110</td>
<td>22</td>
</tr>
<tr>
<td>1960–70</td>
<td>308</td>
<td>29.7</td>
<td>492.7</td>
<td>75</td>
<td>0</td>
<td>26.0</td>
<td>113.4</td>
<td>30</td>
<td>400</td>
<td>100</td>
<td>20</td>
</tr>
<tr>
<td>1970–80</td>
<td>308</td>
<td>17.6</td>
<td>243.6</td>
<td>89</td>
<td>0</td>
<td>15.0</td>
<td>82.6</td>
<td>30</td>
<td>220</td>
<td>30</td>
<td>12</td>
</tr>
<tr>
<td>1980–90</td>
<td>308</td>
<td>24.0</td>
<td>403.0</td>
<td>84</td>
<td>0</td>
<td>21.5</td>
<td>115.5</td>
<td>30</td>
<td>400</td>
<td>10</td>
<td>2</td>
</tr>
</tbody>
</table>

CV: Coefficient of variation
a : Range of sample variogram
C₀ : Nugget of sample variogram
C₁ : Sill of sample variogram
S: Spatial dependence, given by the ratio 100 C₁ / (C₀ + C₁).
IV. CLIMATE AND TREE RINGS AT FORT VALLEY EXPERIMENTAL FOREST

IV.1. Introduction

Ponderosa pine forests around Flagstaff occupy a crucial place in the history and development of modern dendrochronology. It was in these forests, in 1901, that Andrew Ellicott Douglass began collecting wood specimens to test the hypothesis that annual tree growth, as measured by ring width, was influenced by climatic regime, and therefore could be used to reconstruct past climatic fluctuations (Douglass 1909, 1914, and 1919, Webb 1983). Working with ponderosa pine specimens from Flagstaff and Prescott, Douglass elaborated the methods and underlying principles that are still at the core of today's dendrochronology: crossdating, standardizing, quantifying climate-tree growth relations, and reconstructing past ecological variables (Douglass 1919, Webb 1983). Since then, dendrochronology, defined as "the study of the chronological sequence of annual growth rings in trees" (Ferguson 1970), has proved successful in all inhabited continents for a variety of scientific applications, including the exact dating of archaeological specimens and sites, the calibration of radiocarbon dates, the reconstruction of paleoclimatic variables, and the study of phenomena directly or indirectly related to tree growth (Baillie 1982, Schweingruber 1988, Fritts and Swetnam 1989, Hughes 1989).

In this chapter, my objective was to test for temporal modification of climatic regime and/or of climate-tree growth relationship at the study area during the twentieth
century. The hypothesis being tested related closely to the spatio-temporal trends of individual tree growth rates uncovered from repeated forest inventories of the entire study area (Chapter II) and of mapped subplots (Chapter III). In particular, it was assumed that climatic forcing of such trends could be identified only if climate itself had significantly changed over time or if climate-tree growth relations were significantly different from those identified in earlier studies.

IV.1.1. Previous Dendroclimatological Work

Climatic signals in tree rings of ponderosa pines around Flagstaff have been investigated by various authors. Working on a total of 32 trees scattered 12–15 miles around Flagstaff, Douglass (1914) found strong agreement, from 1899 to 1910, between average ring width and total annual precipitation measured at the Flagstaff station, established just a few years before 1899. He found that 12-month total rainfall measured from November of the previous year to October of the current year showed the closest agreement with average ring width. Since November snowfall does not usually melt until the following spring, Douglass argued that snowpack accumulation during the winter months was important for ring formation during the early growing season. Because of moisture shortage during the May–June drought, pines in this region rely primarily on soil moisture derived from snowmelt until the summer monsoon rainfall begins (Douglass 1914). He also added that, in special circumstances, climatic signals could be identified
by just a single tree, and that tree growth in any given year was related to lagged effects of annual precipitation in previous years.

Glock and Agerter (1969) analyzed a total of 159 cores collected at the Fort Valley Experimental Forest from 27 ponderosa pines — 11 of them were from the Gus Pearson Natural Area — with DBH > 50 cm in 1960. They found that total precipitation for June–July of the current year — measured at the Fort Valley station — gave the highest correlation with average ring index over the 1909–1959 period. Winter snowfall, from the previous December to the current March, was also directly related to pine radial growth. They did not find any correlation between precipitation in one year and pine growth in the following year. They concluded that current July precipitation contributed a dominant signal in ponderosa pine tree rings at the study area because it follows a dry period, it is very large compared to the other months, and it comes when trees are actively growing. They also claimed that ponderosa pine growth began declining after 1925 as a consequence of a decline in June–July rainfall after 1923. Annual precipitation also declined after 1930. Glock and Agerter (1969) assumed that sampled pines experienced "moderate to slight" competitive stress, even though they were surrounded by groups of younger pines. They did not remove the age-related decline in ring width. Ring width of pines at the Gus Pearson Natural Area correlated very highly with that of pines from nearby areas; correlation of ring width with June-July precipitation changed from one pine to another.

Glock and Agerter (1969) concluded that ring-width variation could not be used
to reconstruct precipitation, especially when based on a single tree, that lagged effects of precipitation were insignificant, and that summer precipitation, not annual precipitation, most affected annual ring formation. These conclusions seem to refer directly to Douglass' (1914) findings, especially considering Glock and Douglass' professional rivalry (Bannister, pers. comm.). The importance of different seasons and months for ponderosa pine radial growth was later investigated in relation to ecological conditions (Fritts et al. 1965a) and to cambial age (Fritts et al. 1965b). Fritts (1976) concluded that "the response functions for Pinus ponderosa on sites near its arid and low elevation limits in northern Arizona show a more marked correlation of growth with winter precipitation than with summer precipitation, while response functions for the same species on sites at greater distances from the species' arid lower limits show a greater correlation of growth with summer precipitation than with winter precipitation" (ibid., p. 395).

IV.2. Materials and Methods

IV.2.1. Climatic Data

Daily meteorological data recorded at Fort Valley Experimental Forest — 35°16'N, 111°44'W, 2239 m above sea level — include maximum and minimum temperature, total precipitation and amount of snowfall. Daily and monthly data for the 1909–1982 period were obtained from the data tape distributed by the National Climatic
Data Center for the State of Arizona (NOAA 1990a). Data were in tabular format, with each month listed on a single row. Missing values were coded as 999 and precipitation traces were coded as 0. Precipitation and snowfall were integers in $10^{-2}$ inches, temperature was in °F. Because of the large amount of missing values in 1909, that year was removed. Daily data for the 1983–89 period were obtained in computerized format from the Laboratory of Climatology at Arizona State University. Data were in columns, one year per column; missing values — including February 29th on non-leap years — were coded as 999, and precipitation traces were coded as 888.00. Precipitation and snowfall were in inches, with two decimal points, temperature was in °F. Daily data for year 1990 were copied from the Climatological Data bulletins published monthly for the State of Arizona (NOAA 1990b).

Software programs were written in ANSI C (Kelley and Pohl 1990) to convert data from columnar to tabular format and to code all precipitation traces to 0. After format conversion, temperature data from 1910 to 1990 were transformed from °F to °C. Precipitation data for the same period were converted from inches to millimeters. Because of the large amount of missing data, snowfall data were not used in the final analyses. The conversion programs also checked for missing values and for incorrect number of daily values within each month. When more than 9 daily values were missing in a single month, the entire month was considered missing. Monthly summaries were produced from the daily data and checked against the monthly data obtained from the NOAA data tape. All differences greater than 4 mm or 0.2 °C were critically evaluated
and checked against the printed records for that month and year (NOAA 1990b). Monthly averages of daily values were used for maximum and minimum temperature.

Climatic trends were displayed using time-series plots (SAS Institute 1990) and monthly diagrams. Low-frequency variation was displayed by a cubic smoothing spline with a 50% variance reduction at a 70-year period. Statistical significance of monotone temporal trends was tested using the univariate, nonparametric, Mann-Kendall test (Kendall and Gibbons 1990). Monthly data for the Flagstaff station — 35°08'N, 110°40'W, 2135 m above sea level — were also obtained from the NOAA data tape and extended to 1990 using printed records (NOAA 1990b). The climatic regime at Flagstaff was compared to that at Fort Valley for testing data homogeneity (Fritts 1976, p. 254), and then used to estimate missing values in the Fort Valley record. The product-moment coefficient of linear correlation \( r \) (Sokal and Rohlf 1981) was used to evaluate relationships between the two stations, between consecutive months and between precipitation and temperature variables.

IV.2.2. Dendrochronological Data

Dendrochronological sampling consisted of two increment cores extracted from the stem of 58 tagged pines growing on plots 1–29. Two pines, one above and one below 50-cm DBH in 1990, were randomly selected on each plot in order to stratify the sample by two size classes. Large ponderosa pines are often called 'yellow' pines because of the
orange and light brown color of their outer bark; small pines, often called 'blackjacks', are characterized by the dark grey, almost black color of their outer bark. Two increment cores were extracted from each tree about 1.0 m above ground level and 180º from each other whenever possible. Pines on plots 1–14, 16 and 27, i.e. those reported in Avery et al. (1976), were first sampled in 1987 (Swetnam, pers. comm.), and later resampled to extend their tree-ring record until 1990. Two randomly selected pines were also cored on each of the remaining plots, i.e. 15, 17–26 and 28–29. Polar coordinates of each cored pine were obtained in the field using compass and measuring tape. Polar coordinates were converted into x-y coordinates with origin in the southwest corner of the area, and then into UTM (Universal Transverse Mercator) coordinates. Size of sampled pines was tested for spatial autocorrelation using geostatistical methods (Chapter III).

A total of 116 wood cores were collected between November 1990 and July 1991. All increment cores were transported to the laboratory, air dried, and glued to wooden mounts after vertically aligning the xylem tracheids. Mounted cores were mechanically sanded, then polished by hand with progressively finer sandpaper, up to 400–500 grid type, until the smallest rings were clearly visible at 10x magnification. Ring patterns were visually crossdated (Douglass 1941, Stokes and Smiley 1968) using a binocular microscope. Crossdating was independently verified by another researcher, then ring widths were measured to the nearest 0.01 mm by means of a sliding micrometer with a computer interface for data acquisition (Robinson and Evans 1980). Dating accuracy was verified using the computer program COFECHA (Holmes 1983).
Crossdated ring-width series were combined into a single tree-ring chronology. Mean and variance of ring-width series are not homogeneous through time, so that ring-width series are non-stationary and heteroscedastic. The removal of non-stationarity and heteroscedasticity by means of computing appropriate ‘ring indices’ is called ‘standardizing’ in the dendrochronological literature (Douglass 1919, Schulman 1956, Fritts 1976, Hughes et al. 1982, Cook and Kairiukstis 1990). This procedure is aimed at correcting for the ‘biological trend’, i.e. the age-related reduction in cambial activity combined with the geometrical constraint to add new layers over a growing bole. It is also intended to minimize growth variation due to phenomena acting at the individual tree or stand level, while maximizing the growth variation related to large-scale forcing factors. The average of all available samples is commonly used to increase the signal-to-noise ratio and to display short- and long-term patterns. If non-stationary ring-width series were averaged together, the final time series might include erratic low-frequency variation caused by the biological trend of individual specimens. Hence, dendrochronological standardization could also be defined as the method used to combine all tree-ring samples into a single chronology. Cook et al. (1990a and 1990b) review and discuss several methods of standardizing ring-width series.

Separate tree-ring chronologies were developed for pines with 1990 DBH ≥ 50 cm — ‘yellow’, ‘large’ or ‘old’ pines — and with 1990 DBH < 50 cm — ‘blackjacks’, ‘small’ or ‘young’ pines. Two different methods were used to model climatic signals and non-climatic noise. The first one was given by the default options of the ARSTAN
software program (Cook and Holmes 1985). Hence, the final chronology was obtained as follows:

$$\bar{\omega}_t = \phi'_p(B) \left[ \Theta_i \left( \phi_p(B) \frac{w + y_1}{y_2} \right) + \alpha \right]$$

with

- $\bar{\omega}_t = \text{chronology value at year } t$;
- $w = \text{crossdated ring width}$;
- $y_1 = \text{modified negative exponential or straight line (Fritts et al. 1969)}$;
- $y_2 = \text{cubic smoothing spline with 50% variance reduction at a 128-year period (Cook and Peters 1981)}$;
- $\phi_p(B) = 1 - \phi_1 B^1 - \ldots - \phi_p B^p = \text{autoregressive operator of order } P \text{ (Box and Jenkins 1976); usually } 0 < P < 5$. Once it is selected, $P$ is the same for all ring-width series, but the autoregressive parameters are estimated separately for each series (Cook and Holmes 1985);
- $\Theta_i = \text{biweight robust mean (Mosteller and Tukey 1977) applied to the } i\text{-values}$, $i = 1, \ldots, n_t$;
- $n_t = \text{number of measured specimens that included year } t$;
- $\alpha = \text{difference between 1.000 and the arithmetic mean of the robust-mean chronology};$
\[ \phi'_{p} = \text{autoregressive operator of order } p, \text{ with } p \leq P; \ p \text{ is usually zero.} \]

In the second, alternative method, ring width was modeled as an exponential function of both a deterministic component — the intrinsic growth trend —, and a stochastic component — the autoregressive process. Hence, the final tree-ring chronology was obtained as follows:

\[
\ddot{\omega}_i = \phi_p(B) \frac{\sum_{i=1}^{n_t} \left[ \ln(w+1) - y \right]_{it}}{n_t}
\]

with

\[ \ln = \text{natural logarithm, used to obtain homoscedastic time series (Davis 1986);} \]
\[ \text{log-values were positive because ring-width was expressed in } 10^{-2} \text{mm, and} \]
\[ \text{the value of 0.01 mm was added to each ring width to avoid taking logarithms of zero values;} \]
\[ y = \text{cubic smoothing spline with 50\% variance reduction at a 121-year period;} \]
\[ \text{this spline leaves in the ring indices 90\% of the variation at a 70-year period, the one of most interest in this study.} \]

Besides reducing heteroscedasticity, the logarithmic transformation emphasizes differences between small rings. As an example, the absolute difference between consecutive ring widths of 0.13 and 0.07 mm has the same value as the difference between 3.13 and 3.07 mm, even though the latter is, in percentage, much smaller than the former. With the log-
transformation, the difference between 0.13 and 0.07 mm becomes 0.56, and the
difference between 3.13 and 3.07 mm becomes 0.02, much smaller than 0.56. Taking the
logarithm of ring widths is equivalent to plotting ring-width series on semi-logarithmic
paper, a method commonly adopted by European dendrochronologists (Schweingruber
1988, p. 51).

Tree-ring chronologies generated by the two above mentioned methods were
'residual' chronologies. 'Standard' chronologies were obtained when no autoregressive
operator was included in the equations. Fitting autoregressive models to remove
autocorrelation from discrete time series is called 'prewhitening' (Box and Jenkins 1976,
p. 379). Residual chronologies are best suited for dendroclimatic studies because they are
free of temporal autocorrelation, which may generate spurious correlations among discrete
time series (Monserud 1986).

IV.2.3. Dendroclimatic Analysis

The relationship between tree growth and climate in 1920–1990 was investigated
by means of correlation analysis and response-function analysis (Fritts et al. 1971, Guiot
1990). Correlation analysis focused on standard and residual tree-ring chronologies as
they related to total precipitation. Based on previous dendroclimatic studies conducted
in the same area (Douglass 1914, Glock and Agerter 1969, Fritts et al. 1965a, 1965b), the
following precipitation variables were considered: annual precipitation, January through
December (TOTP) or November through October (DTOTP); winter precipitation, December through February (WINP) or December through March (GWINP); summer precipitation, June through August (SUMP) or June through July (GSUMP). Time-series plots and the Mann-Kendall test were used to inspect temporal trends of these new variables.

Response functions focused on residual tree-ring chronologies. Since the dependent variable was not autocorrelated, it was assumed that non-spurious climatic signals identifiable in the tree-ring chronology could only refer to a single growing period. At the study area, diameter growth usually begins in the second half of May, and lasts until August or the first half of September (Schubert 1974, p. 16). Response functions of southwestern ponderosa pine are usually computed up to July of the current growing season (Fritts 1974, 1976). According to Pearson (1931, p. 19) diameter growth "is practically over by September 1." A 12-month dendroclimatic window, going backwards from August of the current growth year to the previous September, was chosen to define explanatory variables. Meteorological variables included a moisture indicator, total precipitation, and a thermal indicator, mean temperature or mean minimum temperature or mean maximum temperature. Comparing response functions based on different types of thermal indicators can improve the identification of climatic signals in tree rings (Tessier 1989). The bootstrap method (Efron and Tibshirani 1986, Guiot 1991) was used to compute confidence intervals for parameter estimates. Response function residuals were analyzed graphically and statistically (Morrison 1983) to examine the temporal stability of the model and to check normality assumptions.
IV.3. Results

IV.3.1. Climatic Regime

The Fort Valley station well represents climatic regime of ponderosa pine forests over the Colorado Plateau (Schubert 1974, p. 10–12). The station was moved from its first location, at 2255 m, to a slightly lower one, at 2239 m, between July and August 1946, but data were continuous (NOAA 1990b) and homogeneous. Overall, the daily record included a minimal amount of missing data. Out of a total record length of 29,585 days — 81 years, from 1910 to 1990 —, precipitation was missing in a total of 192 days, maximum temperature was missing in 224 days, and minimum temperature in 219 days. The only months that were completely missing were January and February 1911, March 1978, and, for temperature alone, February and September 1988. Missing daily values were more frequent in winter or, regardless of season, in the last 15 years. The months of December through February accounted for 49% of the missing precipitation values, and for 43% of the missing temperature values. More than half of the missing precipitation values occurred from 1978 to 1990, and more than half of the missing temperature values occurred from 1974 to 1990.

Based on non-missing data from 1910 to 1990, climate at the study area was characterized by cold snowy winters, May–June droughts and July–August monsoon rainfall. Annual precipitation averaged 564 mm and mean annual temperature averaged
6.0 °C. Monthly precipitation averaged 15 mm in June, the driest month, and 82 mm in August, the wettest month. July and August were the only two months with rainfall greater than 0 in every year. Based on mean monthly temperatures, January is the coldest month (average of -3.8 °C) and July is the warmest (average of 17.0 °C). Snowpack accumulation occurs mostly from November through March, even though snow may fall as early as October and as late as May. Monsoon rainfall alleviates moisture stress during the warmest season (Figure 1). Month-to-month variation in total precipitation is high, and no significant correlation exists between total precipitation in any two consecutive months. Monthly mean temperature follows a more regular, bell-shaped pattern over the year (Figure 1), and significant correlation — 0.24 ≤ r ≤ 0.41, p-values ≤ 0.033 — exists between any two consecutive months, with the exception of May–June, June–July, October–November, and November–December. Correlation between precipitation and temperature was significant — 0.001 ≤ p-value ≤ 0.042 — and negative — -0.37 ≤ r ≤ -0.23 — in March, April, October, November, and December.

No long-term trend was evident in the monthly precipitation and temperature record (Figures 2 and 3): the Mann-Kendall test had p-values ≥ 0.082. Time-series autocorrelation from one year to the next was not statistically significant for monthly total precipitation, monthly mean temperature, annual total precipitation, and annual mean temperature. First-order autocorrelation was significant — 0.23 ≤ r₁ ≤ 0.48, p-values ≤ 0.036 — for mean maximum temperature in June, July, and September, and it was significant — 0.27 ≤ r₁ ≤ 0.53, p-values ≤ 0.017 — for mean minimum temperatu-
ture in April, May, June, July, August, November, and December. Mean maximum
temperature and precipitation were significantly — p-values ≤ 0.001 — and negatively
correlated — -0.62 ≤ r ≤ -0.36 — in all months except June, the driest one. Mean
minimum temperature was significantly — p-values ≤ 0.017 — and positively correlated
— 0.26 ≤ r ≤ 0.47 — to precipitation in months when little or no snow is present on the
ground, i.e. in May, June, July, August, September and October. Such relationships are
usually mediated by the direct link between precipitation and cloud cover, which raises
minimum night temperature by trapping outgoing long-wave radiation and lowers
maximum day temperature by reflecting incoming short-wave radiation (Barry and
Chorley 1987, p. 20). The non-significant correlation between precipitation and minimum
temperature during the months with snow on the ground is likely to stem from the
increased albedo and latent heat of liquefaction and sublimation, which do not let
cloudiness raise minimum temperature.

The climatic regime at Flagstaff, based on monthly data for the 1900–1990 period
(Figure 4), is very similar to that at Fort Valley. The Flagstaff record began in the 1890s,
but the early years were eliminated because of missing temperature values. On average,
Flagstaff is a little warmer — mean annual temperature averaged 7.6 °C — and a little
drier — total annual precipitation averaged 531 mm — than Fort Valley, which is about
100 m higher in elevation. According to Pearson (1931, p. 34), Fort Valley is colder than
Flagstaff because the former is closer to the high San Francisco Mountains than the latter.
Also, both stations are located in a cold air drainage, as shown by temperature ‘inversion’
in fall and winter, when mean minimum temperatures at these two stations are often lower than at higher altitudes (Pearson 1931, p. 32). The warmest, coldest, wettest and driest months are the same at both stations. Correlation between Fort Valley and Flagstaff monthly variables is very high — p-value < 0.001 in every month —, although it decreases in July and August because of frequently localized thundershowers. Linear correlation coefficients between total precipitation at Flagstaff and at Fort Valley were ≥ 0.9 from January to April and from September to December, ≥ 0.8 in May and June, and > 0.6 in July and August. Correlations for mean temperature at the two locations were ≥ 0.9 from January to June and from September to December, and > 0.7 in July and August.

IV.3.2. Tree-Ring Chronologies

Sampled pines (Figure 5) were not affected by spatial autocorrelation. Omnidirectional sample variograms of stem DBH and of tree height did not show any evidence of spatial dependence, because variogram values fluctuated randomly with respect to distance (Figure 6). The variogram model was an horizontal line, called a 'pure nugget model' in the geostatistical literature (Chapter III). Increment cores were dated and measured up to ring-year 1990. Because most cores did not go back further than 1570, measured ring widths ranged from 1570 to 1990. The total number of measured rings was 20,197, of which 16,408 measured on large pines, and 4,509
measured on small pines. No dating errors were identified after running the COFECHA program, even though some cores had low correlations with the rest of the sample. Running COFECHA on the combined data set (N = 116) or on each of the two data sets for large and small pines (N = 58 each) produced indistinguishable results in terms of dating.

The oldest sampled tree was pine 124 on plot 18 (Figure 7). This ponderosa pine, located about 50 m east of the highway, was a large dominant growing in a relatively open spot surrounded by dog-hair thickets. The crown was healthy and vigorous; the trunk base leaned about 15° towards east; total height was 33 m. Terrain slope was 5%, with a southwest exposure, and elevation was 2,225 m. The DBH of this tree increased from 95.0 cm in 1920 to 105.4 cm in 1990. Several locally absent rings were identified in the two cores from 1600 to present, when several other samples were available for crossdating. In particular, no ring was present on either core for years 1735, 1748, 1752, 1773, 1782 and 1822.

Rings formed earlier than 1600 were initially dated against the Flagstaff chronology (Douglass 1940, 1947). For best results, some of the specimens used by Douglass himself to build his chronology were retrieved from the Laboratory of Tree-Ring Research collections. Samples FL-9a and b, FL-17a and FL-13b (Douglass 1947) were used to date rings formed from 1505 to 1600. I identified five rings that were locally absent on either core before AD 1600, i.e. 1585, 1573, 1542, 1532, 1506. Only two specimens, FL-13b and MCG-1316b, were available to crossdate rings formed earlier.
than 1500. Dating was reliable back to 1487, which corresponded to a small ring in MCG-1316b, and to a false ring in FL-13b. In my two cores, the 1487 ring and the previous-year ring were both very small. The possibility of a locally absent ring in MCG-1316b and of a true small ring rather than a false ring in FL-13b could not be ruled out based on just those specimens. A break in one of the two cores complicated matters further by creating a gap of at least 8 years (ca. 1455–1462) in the tree-ring record for that core. In the end, I dated the first visible ring as AD 1380±5, hence pine 124 on plot 18 was older than 600 years in 1990. Since the first visible ring did not include the pith, and the two cores were not taken at ground level, the true age was at least 30–50 years greater, up to a possible maximum of about 700 years. Maximum reported age of southwestern ponderosa pine is about 750 years (Swetnam and Brown 1992).

Maximum ages of sampled ponderosa pines were greater than those reported by White (1985). White analyzed a total of 236 pines, and found that only 5 of them were older than 400 years, with a maximum age of 406 years in 1980 (White 1985). The pines he sampled were located on plots 1–3 and 6–11, and usually one core was taken from each tree (White, pers. comm.). The year of the innermost, cross-dated, ring was used to define pine age, even though most cores did not include the stem pith (White, pers. comm.). In the present study, one out of 58 randomly selected pines was older than 600 years, and other 13 pines were most likely older than 400 years. Hence, the percentage of pines older than 400 years was 2% in White’s (1985) study, as opposed to 24% in this study. The old age of trees at the Gus Pearson Natural Area is even more remarkable if
one considers the location and topography of the stand, on both sides of a major highway and on gently undulating terrain. Traditionally, the search for very old, climatically 'sensitive' trees has targeted remote areas on steep, rocky slopes (Schulman 1956, Swetnam and Brown 1992).

A total of four standard and four residual tree-ring chronologies were obtained (Figures 8 and 9). In the 1920–1990 period, the one covered by forest inventories, sample size ranged from 34 to 58 series for the small pines and from 57 to 58 series for the large pines. In both large and small pines, autocorrelation was removed by a third-order autoregressive model, or AR(3), using the ARSTAN method, and by a second-order autoregressive model, or AR(2), using the alternative method. All autoregressive parameters were positive, as usual in coniferous species of temperate climates (Monserud 1986, Biondi and Swetnam 1987). Year-to-year variation was higher in the second half of the twentieth century than in the first half. Low-growth values were more evident in large pines than in small pines, and in the alternative method more than in the ARSTAN method (Figures 8 and 9). For the 1910–1990 period, the one covered by climatic data, linear correlation between any pair of residual chronologies ranged from 0.81 to 0.95 — p-value < 0.001. Standardization seemed to matter less than pine size, as correlations between chronologies developed from the same pines using two different methods — \( r = 0.92–0.95 \) — were slightly greater than correlations between chronologies developed from different pines using the same method — \( r = 0.89–0.91 \).
IV.3.3. Correlation Analysis of Climate and Tree Rings

No annual or seasonal precipitation variable used for this analysis showed a significant trend from 1910 to 1990 — the Mann-Kendall test had p-values ≥ 0.483. No significant autocorrelation was found in the precipitation variables, with the sole exception of June–July rainfall (GSUMP), with a first-order autocorrelation of 0.266 — p-value = 0.026. Annual precipitation from January to December (TOTP) and from November to October (DTOTP, Douglass 1914) were highly correlated — \( r = 0.83 \), p-value < 0.001. Both expressions of annual precipitation showed large year-to-year variation, reached a low-frequency maximum in the 1920s, declined after 1930 until the late 1940s, and did not return to their highest levels until the 1980s (Figure 10). The establishment of the Gus Pearson Natural Area coincided with a wetter than normal period that lasted until about 1940. According to Fritts (1991), the 1907–1916 period was the second wettest decade from 1600 to 1960 in the Western United States.

Summer and winter precipitation fluctuated from 1910 to 1990, showing a tendency to vary in opposite directions (Figure 10), even though negative correlations between summer and winter precipitation were not significant — p-values ≥ 0.054. Summer precipitation from June to July (GSUMP, Glock and Agerter 1969) correlated well with summer precipitation from June to August (SUMP) — \( r = 0.73 \), p-value < 0.001. Winter precipitation from December to March (GWINP, Glock and Agerter 1969) correlated well with winter precipitation from December to February (WINP) —
\[ r = 0.89, \text{ p-value} < 0.001. \] Annual precipitation, especially the one computed from November to October, correlated better with winter precipitation — \( 0.39 \leq r \leq 0.61, \text{ p-values} < 0.001 \) — than with summer precipitation — \( 0.24 \leq r \leq 0.34, \text{ p-values} \leq 0.047 \). Correlations between annual and seasonal precipitation were higher when seasons were defined according to Glock and Agerter (1969).

Time-series plots of the climatic variables confirmed Glock and Agerter's (1969) finding that June–July rainfall (GSUMP) declined after 1923 and that annual precipitation (TOTP) declined after 1930 (Figure 10). June–July precipitation reached a minimum in the 1940s, then increased in the 1950s, and by 1959 it was back to its 1923 level (Figure 10). Hence, variations in June–July precipitation could not be responsible for the decline of ponderosa pine growth identified by Glock and Agerter (1969). Most likely, failure to remove the declining, biological trend from measured ring-width series, combined with ring-width autocorrelation and competition effects, influenced Glock and Agerter's (1969) results. Summer drought occurred not only in the 1940s but also in the 1970s, while winter precipitation was higher than normal (Figure 10). According to Pearson (1950, p. 116) "July rains were very deficient from 1938 through 1945". The twentieth-century decline of pine outgrowth and basal area increment, as well as the incline of pine mortality, accelerated during those two decades (Chapter II). Even though intertree competition was most likely the primary forcing factor of those trends, climatic stress may have periodically enhanced the burden of competitive interactions.

Both standard and residual tree-ring chronologies correlated well with annual
precipitation (TOTP; Table 1), but correlated better when annual precipitation was computed from November to October (DTOTP), as suggested by Douglass (1914). Other things being equal, both expressions of annual precipitation correlated better with residual chronologies than with standard chronologies, and correlations with annual precipitation were higher for large pines than for small pines (Table 1). Winter precipitation (WINP, GWINP) correlated better with tree-ring chronologies for large pines than with those for small pines. Summer precipitation (SUMP, GSUMP) correlated better with tree-ring chronologies for small pines than with those for large pines. Tree-ring chronologies for large pines correlated better with annual precipitation than with winter precipitation, and correlated with June–July precipitation (GSUMP) but not with June–July–August precipitation (SUMP, Table 1). Based on these comparisons, winter snowfall — and associated snowpack accumulation — seems to benefit the large pines relatively more than the small pines, whereas July rainfall would benefit the small pines relatively more than the large pines.

Tree-ring chronologies obtained using the ARSTAN default options had correlations with climatic variables similar to those of tree-ring chronologies obtained using the alternative method (Table 1). Winter precipitation correlated better with the latter chronologies than with the former ones. January to December precipitation (TOTP) usually correlated better with ARSTAN chronologies, but November to October precipitation (DTOTP) usually correlated better with the other chronologies (Table 1). Mean annual temperature was not correlated to any tree-ring chronology.
Differences between correlation coefficients were statistically tested using both Fisher's and Hotelling's z-transformation (Sokal and Rohlf 1981, p. 589–591). For instance, the hypothesis that large and small pines were influenced differently by summer and winter precipitation involved a total of 16 tests, 4 tests for each of the four precipitation variables (SUMP, GSUMP, WINP, and GWINP). Based on computed p-values, there was no evidence on which to reject the null hypothesis. All differences mentioned in the previous paragraphs with regard to coefficients listed in Table 1 were not statistically significant. Differences between correlation coefficients have been used extensively in dendroclimatic and dendroecological studies (e.g. Schulman 1956, Fritts et al. 1965a), even though the statistical significance of such differences was not tested. Therefore, previous studies based on untested differences between correlation coefficients should be carefully and critically evaluated.

Results provided by response functions (Table 2) were consistent with results of correlation analyses. No monthly temperature variable was ever significant, and July precipitation was always highly significant. When mean temperature was used in conjunction with total precipitation (Figures 11 and 12), February snowfall was significant for both large and small pines, but the former were also significantly related to snowfall in October and December of the previous calendar year. It is possible to conclude that both large and small pines were limited by snowpack accumulation and summer monsoon rainfall, but winter snowfall could be slightly more important for large, old pines than for small, young pines (Tables 1 and 2, Figures 11 and 12). The amount of variance
explained by response functions ranged from 0.52 to 0.57, with no consistent difference between the two methods of standardizing ring-width series (Table 2). Significance of monthly climatic variables was usually enhanced when residual tree-ring chronologies were computed by means of the alternative method (Table 2, Figures 11 and 12).

The goodness of fit between the observed and estimated dependent variable was evaluated by means of their difference, i.e. the response function residuals (Figures 13–15). It is possible to notice that the alternative method applied to large pines (L_E) had response function residuals with the greatest variability (Figure 13), quantified by the sample variance and range (Table 3). Bartlett’s test for homogeneity of variances (Sokal and Rohlf 1981, p. 403–405) indicated that variances of the four series were significantly heterogeneous. The F-test was used to compare pairs of variances (Sokal and Rohlf 1981, p. 190), and significance level was adjusted according to Bonferroni’s inequality (Morrison 1983), hence only p-values smaller than $0.05/6=0.008$ were considered significant. Pairs of variances were significantly different — p-values $< 0.001$ — only when L_E was involved.

Variability of response function residuals seemed greater in the second half of the twentieth century (Figure 13). The sample variance and range before 1955 were always smaller than those after 1955 (Table 3). The F-test for comparing variance in 1921–1955 to variance in 1956–1990 had p-values of 0.004 for S_A, 0.030 for S_E, 0.013 for L_A and 0.022 for L_E. According to Bonferroni’s adjustment, significant p-values had to be no greater than $0.05/4=0.013$, hence the hypothesis of no difference could only be rejected
for S_A and L_A, i.e. the chronologies developed using the ARSTAN method.

Normality of response function residuals was tested using the Shapiro and Wilk (1965) test (Table 3). In this test, greater p-values provide stronger support to the hypothesis of normality, hence normality was in doubt only for the 1921–1990 residuals from the L_E chronology (Table 3). Histograms and box plots (Figure 14) confirmed that response function residuals for the alternative method applied to large pines (L_E) followed a distribution less bell-shaped than the other residuals. Extreme residual values were positive for the ARSTAN method and were negative for the alternative method (Figure 14). Plotting residuals against estimates (Figure 15) produced additional evidence that the L_E residuals were the most irregular ones. Linear correlation between residuals and estimates was never significant — p-values $\geq 0.458$. In conclusion, analysis of response function residuals did not indicate violations of normality assumptions, and suggested that the ARSTAN method is better than the alternative method for producing a dendroclimatic record from ring-width series of large ponderosa pines.

IV.4. Conclusions

No temporal trend was identified in monthly and annual climatic variables during the 1910–1990 period. Climate fluctuated at the decadal and yearly time scales, but the decline of individual growth rates identified in repeated forest inventories (Chapter II) and the decrease over time of spatial dependence of stem increment (Chapter III) could not
be related to any long-term change in climate at the study area. It is possible that
summer drought during the 1940s and 1970s accelerated the decline of pine outgrowth
and basal area increment displayed in Figures 12 and 23, Chapter II, and that it also
favored the increased pine mortality displayed in Figure 9, Chapter II. Further research
is needed to test these hypotheses, and could be based on the inclusion of appropriate
density and climatic factors in the mixed linear model described in Chapter II.

Correlation and response-function analyses indicated that precipitation signals
dominated the influence of climatic regime on annual ring formation. Climate-tree growth
relations identified in this study agreed with previous dendroclimatic studies in the
Flagstaff area carried out by Douglass in 1914 and by Glock and Agerter in 1969. This
provides strong supporting evidence to the hypothesis that climate-tree growth relations
had not significantly changed over the twentieth century. Results were also consistent
regardless of the standardization method used to develop the average tree-ring chronology.
Annual growth of both large and small pines at this forest interior site was positively
related both to winter snowfall — and associated snowpack accumulation — and to July
rainfall. Even though favorable climatic conditions contributed to the successful
regeneration pulses that increased stand density, the use of residual tree-ring chronologies
— such as those generated by the ARSTAN program — computed from a large sample
size is a plausible guarantee that dendroclimatic reconstructions at the yearly time scale
will be independent of site conditions.

Dendroclimatic results were not completely unrelated to the endogenous
transformation of site structure over the twentieth century. Variance of residuals from response functions showed a tendency to increase in the most recent decades. If the climatic control of annual wood production in individual trees remained essentially unaltered, as stated in the previous paragraph, stronger deviations from the average climate-tree growth relations may be attributed to increased stand density and competitive interactions. Tree growth may have been more limited by climate than by competition during the first part of the century, but with increased crowding, the influence of climate on tree growth may have been reduced. Further research, e.g. extensive tree-ring analysis of age distribution and growth rates of pine clusters, could provide clues about the interaction of climate, cambial age and stand structure for controlling tree growth variation.
FIGURE IV.1. Climatic diagrams for the 1910–1990 period at Fort Valley. Monthly values are plotted by month and year, using as reference line for each month the arithmetic mean of available data.
FIGURE IV.2. Time-series plots of monthly total precipitation for the 1910–1990 period at Fort Valley.
FIGURE IV.3. Time-series plots of monthly mean temperature for the 1910–1990 period at Fort Valley.
FIGURE IV.4. Climatic diagrams for the 1900–1990 period at Flagstaff. Monthly values are plotted by month and year, using as reference line for each month the arithmetic mean of available data.
FIGURE IV.5. Map of pines cored on plots 1-29; origin of x-y coordinates is the southwest corner of the area. Circle diameter is proportional to stem diameter in 1991 and is on a different scale than stem coordinates.
FIGURE IV.6. Histogram and box plot (left), together with omnidirectional sample variogram (right) for 1991 stem diameter (DBH) and height of pines cored on plots 1–29. The histograms are bimodal because of pine selection strategy, and the sample variograms indicate no spatial autocorrelation in the data.
Digitized image of tree rings formed, from right to left, in 1645–1656 within the oldest sampled pine. Year 1654 is absent in core A (above) and is micro, hence barely visible, in core B (below). The image exemplifies that individual xylem cells have to be visible for crossdating to be reliable.
Time-series plots of standard and residual tree-ring chronologies for the 1570–1990 period at the study area. A dashed vertical line marks year 1920. S_A: small pines, ARSTAN method; S_E: small pines, alternative method; L_A: large pines, ARSTAN method; L_E: large pines, alternative method.
FIGURE IV.9. The same as Figure 8, restricted to the 1910–1990 period.
FIGURE IV.10. Time-series plots of total precipitation variables for the 1910–1990 period at Fort Valley. TOTP: annual precipitation from January to December; DTOTP: annual precipitation, from the previous-year November to the current-year October; GWINP: winter snowfall, from the previous December to the current March; WINP: winter snowfall, from the previous December to the current February; SUMP: summer rainfall, from June to August; GSUMP: summer rainfall in June and July. Years 1923, 1930 and 1959 are identified by dashed lines. Low-frequency variation is represented by a cubic smoothing spline (SAS Institute 1990).
Dendroclimatic response functions for 1921–1990 of (a) pines with 1990 DBH ≥ 50 cm, and (b) pines with 1990 DBH < 50 cm. Residual tree-ring chronologies were obtained using the ARSTAN method (see text for details). The 12-month dendroclimatic window is on the x-axis and ranges from September of the previous year to August of the current year. Bootstrapped 95% confidence intervals (C.I.) for each monthly climatic variable are on the y-axis.
FIGURE IV.12. The same as Figure 11, with the exception that residual tree-ring chronologies were obtained using the alternative method (see text for details).
FIGURE IV.13. Time-series plots of residual tree-ring chronologies (above) used in (solid line) and estimated by (dashed line) response functions for the 1921–1990 period. The response function residuals (below) are the difference between observed (OBS.) and estimated (EST.) residual chronologies. A dashed vertical line marks year 1955, dotted horizontal lines mark the null mean (above) and the one-standard deviation intervals around the null mean (below). S_A: small pines, ARSTAN method; S_E: small pines, alternative method; L_A: large pines, ARSTAN method; L_E: large pines, alternative method.
Residual Chronologies

Response Function Residuals
FIGURE IV.15. Graph of response function residuals (OBS.—EST.) versus the response function estimates (EST.) for the 1921–1990 period. Dotted lines mark the null means. S_A: small pines, ARSTAN method; S_E: small pines, alternative method; L_A: large pines, ARSTAN method; L_E: large pines, alternative method.
TABLE IV.1. Linear correlation coefficients between tree-ring chronologies (Figure 8) and total precipitation variables (Figure 9) for the 1921–1990 period (N = 70).

<table>
<thead>
<tr>
<th>Precipitation Variable</th>
<th>Standard Chronologies</th>
<th>Residual Chronologies</th>
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</thead>
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<td></td>
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<td>TOTP</td>
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<td>DTOTP</td>
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<td></td>
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<td>.0001</td>
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<td></td>
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<td>.0006</td>
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<td>SUMP</td>
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<td>0.12</td>
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<tr>
<td></td>
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</tr>
<tr>
<td>GSUMP</td>
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<td>0.35</td>
</tr>
<tr>
<td></td>
<td>.0005</td>
<td>.0030</td>
</tr>
</tbody>
</table>

The p-value is given underneath each coefficient.

TOTP: Annual precipitation, from January to December.
DTOTP: Annual precipitation, from November of the previous year to October of the current year.
WINP: Winter precipitation, from December to February.
GWINP: Winter precipitation, from December to March.
SUMP: Summer precipitation, from June to August.
GSUMP: Summer precipitation, from June to July.

L_A, S_A: Tree-ring chronology developed using the ARSTAN method for pines with 1990 DBH, respectively, ≥ 50 cm and < 50 cm.
L_E, S_E: Tree-ring chronology developed using the alternative method for pines with 1990 DBH, respectively, ≥ 50 cm and < 50 cm.
TABLE IV.2. Summary of significant predictors in bootstrapped response functions computed for the 1921–1990 period between pine tree-ring chronologies and selected climatic variables.

<table>
<thead>
<tr>
<th>Tree-Ring Chronology</th>
<th>Monthly Climatic Variables</th>
<th>R²</th>
<th>Significant Monthly Precipitation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Large Pines, ARSTAN method</td>
<td>Mean Temperature, Total Precipitation</td>
<td>0.54</td>
<td>OCT, DEC, FEB, JUL</td>
</tr>
<tr>
<td></td>
<td>Mean Min. Temp., Total Precipitation</td>
<td>0.57</td>
<td>OCT, APR, JUL</td>
</tr>
<tr>
<td></td>
<td>Mean Max. Temp., Total Precipitation</td>
<td>0.52</td>
<td>OCT, FEB, JUL</td>
</tr>
<tr>
<td>Small Pines, ARSTAN method</td>
<td>Mean Temperature, Total Precipitation</td>
<td>0.54</td>
<td>FEB, JUL</td>
</tr>
<tr>
<td></td>
<td>Mean Min. Temp., Total Precipitation</td>
<td>0.54</td>
<td>OCT, MAY, JUL</td>
</tr>
<tr>
<td></td>
<td>Mean Max. Temp., Total Precipitation</td>
<td>0.53</td>
<td>FEB, JUL</td>
</tr>
<tr>
<td>Large Pines, Alternative method</td>
<td>Mean Temperature, Total Precipitation</td>
<td>0.53</td>
<td>OCT, DEC, FEB, JUL</td>
</tr>
<tr>
<td></td>
<td>Mean Min. Temp., Total Precipitation</td>
<td>0.55</td>
<td>OCT, DEC, FEB, MAR, MAY, JUL</td>
</tr>
<tr>
<td></td>
<td>Mean Max. Temp., Total Precipitation</td>
<td>0.52</td>
<td>FEB, JUL</td>
</tr>
<tr>
<td>Small Pines, Alternative method</td>
<td>Mean Temperature, Total Precipitation</td>
<td>0.56</td>
<td>FEB, MAY, JUL</td>
</tr>
<tr>
<td></td>
<td>Mean Min. Temp., Total Precipitation</td>
<td>0.54</td>
<td>OCT, MAY, JUL</td>
</tr>
<tr>
<td></td>
<td>Mean Max. Temp., Total Precipitation</td>
<td>0.56</td>
<td>MAY, JUL</td>
</tr>
</tbody>
</table>

*: p-value < 0.05.
All significant precipitation variables had a positive coefficient.
No temperature variable was ever significant.
### TABLE IV.3. Variability of response function residuals.

<table>
<thead>
<tr>
<th>PERIOD</th>
<th>SAMPLE VARIANCE</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>S_A</td>
<td>S_E</td>
<td>L_A</td>
<td>L_E</td>
</tr>
<tr>
<td>1921–1990</td>
<td>0.015</td>
<td>0.021</td>
<td>0.026</td>
<td>0.070</td>
</tr>
<tr>
<td>1921–1955</td>
<td>0.008</td>
<td>0.013</td>
<td>0.016</td>
<td>0.043</td>
</tr>
<tr>
<td>1956–1990</td>
<td>0.022</td>
<td>0.028</td>
<td>0.037</td>
<td>0.097</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>RANGE</th>
<th>S_A</th>
<th>S_E</th>
<th>L_A</th>
<th>L_E</th>
</tr>
</thead>
<tbody>
<tr>
<td>1921–1990</td>
<td>0.743</td>
<td>0.731</td>
<td>0.949</td>
<td>1.425</td>
</tr>
<tr>
<td>1921–1955</td>
<td>0.353</td>
<td>0.468</td>
<td>0.494</td>
<td>0.814</td>
</tr>
<tr>
<td>1956–1990</td>
<td>0.743</td>
<td>0.731</td>
<td>0.949</td>
<td>1.425</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>SHAPIRO-WILK P-VALUES</th>
<th>S_A</th>
<th>S_E</th>
<th>L_A</th>
<th>L_E</th>
</tr>
</thead>
<tbody>
<tr>
<td>1921–1990</td>
<td>0.443</td>
<td>0.793</td>
<td>0.781</td>
<td>0.112</td>
</tr>
<tr>
<td>1921–1955</td>
<td>0.345</td>
<td>0.217</td>
<td>0.726</td>
<td>0.335</td>
</tr>
<tr>
<td>1956–1990</td>
<td>0.245</td>
<td>0.858</td>
<td>0.588</td>
<td>0.306</td>
</tr>
</tbody>
</table>

S_A: small pines, ARSTAN method.  
S_E: small pines, alternative method.  
L_A: large pines, ARSTAN method.  
L_E: large pines, alternative method.
V. DENDROCHRONOLOGICAL TREND DETECTION: A GRAPHICAL CASE STUDY

V.1. Introduction

Both repeated forest inventories and dendrochronological data provide non-destructive methods to obtain historical information on tree growth from stem diameter. The main advantage of dendrochronology for historical reconstructions is dating accuracy. Fritts and Swetnam (1989) define dendrochronology as "the systematic use of tree-ring cross-dating, a procedure that uses variability of ring characteristics to establish the exact year in which each ring was formed". They describe and discuss applications of crossdating in ecological studies, and point out that significant estimation errors arise when ring counting is preferred to crossdating. Numerical, graphical and visual techniques of crossdating have been developed to accurately assign calendar years to xylem layers (Douglass 1941, Stokes and Smiley 1968, Baillie and Pilcher 1973, Holmes 1983, Munro 1984, Wigley et al. 1987, Van Deusen 1990a, Yamaguchi 1991, Van Deusen and Reams 1993). Crossdating is not commonly used in forest mensuration studies, but its practical importance should not be overlooked. For instance, accurate measurements of tree age translate into more refined data on forest stand growth, which in turn allow more efficient utilization of forest resources (Zeide 1993).

Once crossdated ring widths are measured, it is necessary to reduce them into a
manageable representation of historical trends. The objective of this chapter was to visually compare temporal growth trends outlined by different methods of producing an average tree-ring chronology. It has been suggested that the relationship between tree rings and climate could best be quantified without reducing ring-width series into an average ring-index chronology (Van Deusen 1990b, Visser and Molenaar 1990, Eriksson et al. 1990). Even though this may be true, trend detection sometimes relies on tree rings without climatic data (e.g. Hornbeck et al. 1988, Swetnam and Lynch 1989, Reams and Huso 1990, Cook 1990). In these cases, or when dating is the major objective of the study, it is still necessary to produce an accurate representation of average year-to-year tree-ring patterns.

Different standardization methods may produce very similar tree-ring chronologies, especially if no time-series autocorrelation is left in the average chronology (Chapter IV). Trend detection, however, requires a distinction between low-frequency growth variation related to cambial age and that related to large-scale forcing factors. When this is the case, reconstruction of climatic regime and forest productivity may become controversial. For instance, in their analysis of Pinus sylvestris L. tree-ring data from northern Sweden, Briffa et al. (1990) first found little evidence for the Medieval Warm Epoch and for an extended Little Ice Age. They later (1992) reanalyzed the same data by means of a different standardization option and recognized a period of Medieval Warmth in the tenth and eleventh centuries, as well as a cold period from the late sixteenth to the middle eighteenth century.
Dendrochronologists and forest mensurationists are both interested in spatio-temporal patterns of forest growth and in their ecological implications. Traditionally, mensurationists have focused on quantifying present and future timber resources in relation to site characteristics and management practices. Dendrochronologists have concentrated on reconstructing environmental variables — precipitation, temperature, air pressure, streamflow, drought severity, sunshine, etc. — and dating past events — fire, insect outbreaks, volcanic eruptions, landslides, floods, windthrows, earthquakes, frosts, etc. — recorded in annual xylem layers of selected trees (Bartholin et al. 1992, Jacoby and Hornbeck 1987).

Forest mensurationists are interested in future, absolute, average values of stand growth, whereas dendrochronologists are interested in past, relative, year-to-year values of tree growth. This partly explains why mensurationists avoid computing the dimensionless ring indices used by dendrochronologists and prefer to convert ring widths into ring areas, or basal area increments, to quantify temporal trends (Hornbeck et al. 1988). Still, LeBlanc (1990) found that average ring indices at breast height correlated strongly with ring indices computed for the whole stem. Thammincha (1981) found good agreement between his annual ring-index series for southern Finland and the data from National Forest Inventories. He was also able to improve accuracy of stand growth predictions by including information on inter-annual variation derived from tree-ring data.

The real advantage of dendrochronological data over forest inventory data lies in the analysis of year-to-year growth patterns. Inventory data on permanent plots are
usually collected at 5-to-10-year intervals. Hence, interpolation between successive inventories is needed to compute yearly growth values (Eriksson et al. 1990), but because of the smooth pattern of interpolated annual growth rates, the effect of year-to-year environmental variation on tree growth is likely to remain undetected. Dendrochronological models are then needed to empirically quantify the influence of regional forcing factors, such as climatic regime, upon annual wood production (Graumlich 1989).

V.2. Materials and Methods

V.2.1. Dendrochronological Data

The same tree-ring data used for identifying climatic signals (Chapter IV) were used to quantify temporal growth trends. Every ring-width series was transformed into a ring-area series, as follows:

\[ a_t = \frac{w_t}{100} \left( w_t + 2 \sum_{i=0}^{t-1} w_i \right) \]

with \( a_t \) = ring area \( (cm^2 \pi^{-1}) \) at year \( t \); \( w_t \) = ring width (mm) at year \( t \); \( w_i \) = crossdated ring width (mm), \( i = 1, \ldots, t-1 \); \( w_0 \) = distance (mm) between the stem pith and the innermost measured ring. When a core did not include the pith, \( w_0 \) was estimated using circles to approximate tree rings (Applequist 1958). The two ring-area series from the
same pine were averaged to quantify current annual basal area increment. For comparison
with data from forest inventories (Chapter II), the 10-year periodic basal area increment
(PBAI) was computed as the 10-year sum of the current annual basal area increment,
from 1921 to 1990.

Dendrochronology provides superior estimates of annual growth rates in individual
trees because of its precision, accuracy and resolution of ring-width dating and measuring.
Hence, the PBAI values computed from ring-area series were used as 'true' values to
estimate the amount of error involved in estimating PBAI values from forest inventories.
Two measures of error were used, as follows:

\[ MEE\left(\text{cm}^2\text{yr}^{-1}\right) = \sqrt{\frac{\sum_{i=1}^{n_i} \sum_{t=1}^{n_t} (PBAI_1 - PBAI_2)^2}{n_i n_t}} \]

and

\[ MPE(\%) = \frac{\sum_{i=1}^{n_i} \sum_{t=1}^{n_t} \left(100 \frac{PBAI_1 - PBAI_2}{PBAI_1}\right)^2}{n_i n_t} \]

with \( MEE \) = mean estimation error; \( PBAI_1 \) = 10-year periodic basal area increment
computed from ring-area series; \( PBAI_2 \) = 10-year periodic basal area increment computed
from forest inventories; \( n_i \) = number of pines; \( n_t \) = number of time intervals; \( MPE \) = mean
percentage error.
V.2.2. Standardization Methods

The existence of temporal trends implies autocorrelation in the time series (Box and Jenkins 1976). Since decadal or century-long patterns are obliterated if autocorrelation is removed by fitting Box-Jenkins models, ring-width series were not prewhitened. The final chronology was computed as the arithmetic average of ring indices, computed in various ways. Cook et al. (1990a) employed a robust mean to minimize the influence of extreme values on the average chronology. Because of the large number of samples available in this study — N > 30 from 1920 to 1990 — the simple arithmetic average was used in order to compare different standardization methods for their own 'robustness' (Lehmann 1975, p. 189). Trends obtained by arithmetically averaging ring widths, rather then ring indices, were used as a baseline for comparisons.

The following standardization options were considered:

(0) normalization (Van Deusen et al. 1991), the closest option to no standardization at all:

\[
\bar{I}_t = \frac{\sum_{i=1}^{n_t} \left( \frac{w_i - \bar{w}}{s_w} \right)_i}{n_t}
\]

with

\[
\bar{I}_t = \text{average ring index at year } t ;
\]
\( n_t = \text{number of specimens } i \text{ that included year } t ; \)
\( w_i = \text{ring-width measurement } (10^{-2} \text{ mm}) \text{ at year } t \text{ on the } i\text{-th specimen;} \)
\( w = \text{arithmetic mean of the } i\text{-th ring-width series;} \)
\( s_w = \text{standard deviation of the } i\text{-th ring-width series;} \)

(1) growth curve and division (Douglass 1919):

\[
\overline{I}_t = \frac{\sum_{i=1}^{n_t} \left( \frac{w}{y} \right)_{ii}}{n_t}
\]

with additional categories given by the type of growth curve, as follows:

(a) \( y = \) modified negative exponential or straight line (Fritts et al. 1969);

(b) \( y = \) cubic smoothing spline (Cook and Peters 1981) with 50% variance reduction at a 50-year period; this spline leaves in the ring-index series 90% of the variation at a 29-year period;

(c) \( y = \) cubic smoothing spline with 50% variance reduction at a 121-year period; this spline leaves in the indices 90% of the variation at a 70-year period, the one of most interest in this study;

(2) double detrending (Cook and Holmes 1985, Chapter IV):

\[
\overline{I}_t = \frac{\sum_{i=1}^{n_t} \left( w \div \frac{y_1}{y_2} \right)_{ii}}{n_t}
\]
with \( y_1 = \) modified negative exponential or straight line of any slope; \( y_2 = \) cubic smoothing spline with 50% variance reduction at a 128-year period;

(3) exponential model (Biondi 1993, Chapter IV):

\[
\bar{I}_t = \frac{\sum_{i=1}^{n_t} [\ln(w+1) - y]_{it}}{n_t}
\]

with \( y = \) cubic smoothing spline with 50% variance reduction at a 121-year period;

(4) average of normalized splines (modified from Sheppard 1991):

\[
\bar{I}_t = \frac{\sum_{i=1}^{n_t} \left( \frac{y_i - \bar{y}}{s_y} \right)_{i}}{n_t}
\]

with \( y = \) cubic smoothing spline with 50% variance reduction at a 40-year period — this spline incorporates 90% of the variation at a 70-year period, the one of most interest in this study;

(5) average of normalized ring-area series (modified from Phipps and Whiton 1988):

\[
\bar{I}_t = \frac{\sum_{i=1}^{n_t} \left( \frac{a_i - \bar{a}}{s_a} \right)_{i}}{n_t}
\]

(6) log transform and first differencing (Van Deusen 1991):
with $\omega = w + 0.01$ mm;

\begin{equation}
\bar{t}_t = \frac{\sum_{i=1}^{n_t} \left( \ln \frac{\omega_t}{\omega_{t-1}} \right)_i}{n_t}
\end{equation}

For classification purposes it may be useful to distinguish methods that require fitting a growth curve from those that do not. Options 1, 2, and 3 fall in the former category, whereas options 0, 4, 5, 6, and 7 fall in the latter one. Other grouping criteria may be the presence of a logarithmic transformation — options 3, 6, and 7 —, the use of normalized series — options 0, 4, and 5 —, or the computation of indices as ratios — options 1 and 2. Each standardization option was first applied to the pines with 1990 DBH $< 50$ cm — ‘small’ or ‘young’ pines —, then to the pines with 1990 DBH $\geq 50$ cm — ‘large’ or ‘old’ pines —, and finally to all of the pines. Every crossdated series was treated equally in the standardization process.

V.3. Results and Discussion
V.3.1. Tree-ring Data

Time-series plots of ring-width series showed a declining trend from 1920 to 1990 (Figures 1 and 2). The decline was more evident in pines with 1990 DBH < 50 cm, although their ring widths from 1920 to 1990 remained larger than those of pines with 1990 DBH ≥ 50 cm (Figure 2). Apparently, variability of ring widths in large pines was lower in the 70 years after 1920 than in the 70 years before 1920 (Figures 1b and 2b). Temporal growth trends were different for ring-area series (Figures 3 and 4). The declining trend from 1920 to 1990 was still visible in the large pines (Figure 4b), but not in the small pines (Figure 4a), which appeared to fluctuate around a more constant level than the large pines. Ring areas of large pines showed an unprecedented peak around 1910, but their variability did not seem to decrease after 1920 (Figures 3b and 4b). Time-series plots of 10-year periodic basal area increment (PBAI) from 1920 to 1990 (Figures 5 and 6) were similar to those computed from forest inventory data (Chapter II). Growth rates of large pines declined more than those of small pines. Large pines had larger PBAI than small pines, even though statistical models applied to forest inventory data for the entire stand had indicated that in the last decades PBAI was greater in small pines than in large pines (Chapter II).

Comparisons between PBAI of individual trees during a specific period may have been affected by error involved in computing PBAI from repeated DBH measurements. The mean estimation error of computing PBAI from forest inventories rather than from
dendrochronological data was greater for small pines — 14.28 cm$^2$\text{-1} — than for large pines — 18.18 cm$^2$\text{-1}. The mean percentage error was -61% for small pines, and -8% for large pines. Therefore, forest inventories over-estimated periodic basal area increment, especially for pines with 1990 DBH < 50 cm. Shrinking of increment cores after drying could account for a limited portion of the over-estimation error. Pith location was usually easier to identify in pines with 1990 DBH < 50 cm, hence ring-area series were more accurate for small pines than for large pines. Bark furrows are usually deeper and narrower in ‘blackjacks’ than in ‘yellow pines’, hence diameter measures were less accurate for small pines than for large pines. Irregularity of the bark surface and stem geometry, combined with the low precision, accuracy and resolution of diameter tape measurements compared to tree-ring data, certainly contributes to measurement error, but it is unlikely to produce such a large over-estimation error.

A major difference between computing growth rates from repeated forest inventories and from increment cores is that the former include both wood and bark increment, whereas the latter quantify wood increment only. Presumably, bark production and shedding is not balanced in small pines as it is in large pines, so that diameter increment of small pines is largely related to bark growth rather than to xylem growth. Perhaps ‘blackjacks’ retain their bark longer than ‘yellow pines’ because they are shorter, hence they have a higher risk of being killed by surface fires. In fire-controlled ecosystems, natural selection and evolution have resulted in several fire-adapted traits of forest species (Kozlowski \textit{et al.} 1991, p. 415–419), and the amount of fire-resistant bark
retained by trees of different age may simply be another one of these traits. Relative errors computed in this study suggest that bark growth of small pines may account for as much as 50% of their basal area increment obtained from repeated DBH measurements. This estimation error should not change considerably with time for a given size class, hence it is not likely to affect the statistical assessment of temporal growth trends presented in Chapter II.

V.3.2. Tree-ring Chronologies

Different standardization options produced chronologies with different temporal trends. The average of normalized ring-width series (Figures 7 and 8) showed a period of larger-than-normal growth in the early 1900s, followed by a period of lower-than-normal growth for both small and large trees. The decline began around 1920, levelled off after 1970, and, for the small pines, began reversing in the last few years preceding 1990 (Figure 8). These temporal trends were consistent with those identified from time-series plots of ring-width series (Figures 1 and 2). They were also consistent with trends detected graphically and statistically for periodic basal area increment of individual pines. Periodic basal area increment decreased over time regardless of tree size (Chapter II), and this agreed with the overall decreasing trend of ring-width series from 1920 to 1990.

Tree-ring chronologies developed by computing ring indices as ratios did not show any decline over time (Figures 7–12). When the growth curve was a negative exponential
— option 1a —, the final chronology for small pines displayed an exponential increase after 1980 (Figures 7 and 8). Since ring-width series ended in a low-growth period, dividing the ring width by the curve value artificially inflated the final part of the tree-ring chronology. A flexible cubic spline — option 1b — obliterated all the low-frequency variation of interest in this particular study (Figures 9 and 10), whereas a stiff cubic spline — option 1c — produced tree-ring chronologies (Figures 9 and 10) very similar to those generated by the negative exponential curve. Double detrending produced large ring indices in the most recent years of the chronology (Figures 11 and 12), even though they were not as large as those produced by single detrending (Figures 7–10). Tree-ring chronologies developed by computing ring indices as differences did not show any decline over time (Figures 11 and 12). With this option, a stiff cubic spline did not generate large ring indices in recent years. Low-growth years were greatly emphasized, especially before 1800 (Figure 11). Chronologies for both large and small pines showed an increasing trend in recent years (Figure 12). Among standardization options that required fitting a growth curve to model the biological trend, fitting the spline to log-transformed ring widths and then computing ring indices as deviations from the growth curve, was the most robust method with respect to end-series computational problems.

Temporal trends of known frequency were clearly represented by the average of normalized, 40-year, cubic smoothing splines — option 4 (Figures 13 and 14). Tree rings were larger than normal in the first 3–4 decades of the 1900s, and smaller than normal ever since (Figure 14). The establishment of the Gus Pearson Natural Area coincided
with the largest peak of annual growth as well as with the beginning of the longest
growth decline in the last three centuries (Figure 13). Tree-ring chronologies derived
from normalized ring-area series — option 5 — highlighted the difference between
temporal trends of large and small pines (Figures 13 and 14). Large pines showed a
unique growth surge in the early 1900s followed by a continued decline until about 1980
(Figure 14). Small pines showed a less dramatic growth increase in the early 1900s
followed by a less dramatic decline up to about 1980, when growth rates began increasing
again (Figure 14). Inferences and comparisons of temporal trends for trees of different
age/size classes are more accurate when ring-area series are used, because ring-area series
are less dependent on cambial age than ring-width series (Phipps 1979).

Standardizing by means of log-transforming ring widths and then computing the
difference between adjacent values — options 6 and 7 — removed all trends (Figures 15
and 16). These options also produced extreme, adjacent values of opposite sign — the
'rebound' effect — especially when differencing was repeated twice — option 7 (Figures
15 and 16). Differencing implies the assumption that temporal trends are generated by
a nonstationary stochastic process (Box and Jenkins 1976, p. 92). Because of the basic
temporal unidirectionality of tree growth, which inevitably goes to zero when the tree
dies, and of the geometrical constraint to add new layers over a growing bole, tree-ring
formation cannot be considered as a purely stochastic process, and it is best described by
including a deterministic trend component. It is possible that the Kalman filter, used to
estimate parameters of stochastic models relating ring widths to long-term trend and year-
to-year climatic variation (Van Deusen 1989, Visser and Molenaar 1988), might overcome the limitations of the differencing approach.

V.4. Conclusions

Repeated forest inventories over-estimated periodic basal area increment, especially for pines with 1990 DBH < 50 cm. When periodic basal area increment computed from crossdated ring-width series was compared to periodic basal area increment computed from repeated DBH measurements, the mean percentage error was -61% for small pines, and -8% for large pines. Therefore, growth rates of small pines computed from forest inventories were, on average, artificially inflated when compared to those of large pines. Presumably, small and large pines have different patterns of bark increment and/or retention. For trend detection, repeated forest inventories contain information on growth rates of individual trees as well as of the entire stand, but they mix both bark and wood increment, and lack the temporal resolution and accuracy of dendrochronological data. On the other hand, the high cost of dendrochronological data prevents spatial replication from being as large as in forest inventories.

Overall, the twentieth century was characterized by rather peculiar temporal trends when compared to the previous two or three centuries. To complicate matters further, dendrochronological trend detection was influenced by the standardization method. The average of normalized ring-width series and of flexible cubic smoothing splines outlined
a nonlinearly decreasing trend from 1920 to 1980 for both large and small pines. The same trend was present in the average of normalized ring-area series for large pines, but was almost absent in the average of normalized ring-area series for small pines. Computing tree-ring indices as ratios between ring width and a growth curve — negative exponential or stiff cubic spline — generated an upward trend in the most recent portion of the chronology. Computing indices by first- or second- differencing removed all low-frequency variation. Double detrending and the exponential model resulted in tree-ring chronologies where the post-1920 decline and the recent increase were less pronounced.

Based on average ring-width and ring-area series, annual growth of sampled pines, especially those with 1990 DBH less than 50 cm, increased in recent years after reaching minimum values in the late 1970s (Figures 8, 12 and 14). This recent trend paralleled an increase of summer precipitation in the 1980s (Figure 9, Chapter IV). According to dendroclimatic analyses, July monsoon rainfall benefits ponderosa pine growth (Chapter IV). It is remarkable, and in need of further testing, that these trees still respond to climatic variation despite the high density of the stand and the consequent reduction of average growth rates (Chapter II).

The identification of ‘abnormal’ long-term decline in tree radial growth has to be preceded by the definition of the ‘normal’, or expected, long term decline caused by the biological trend (Fritts and Swetnam 1989, Federer and Hornbeck 1987). The negative exponential curve reflects expected features of radial increment in open-grown trees (Fritts 1976). The smoothing cubic spline was proposed to model expected low-frequency
variation related to factors acting on individual trees and stands, especially in dense, uneven-aged forest stands where shade-tolerant species may respond to release effects (Cook 1987). The present case study, albeit based on graphical rather than quantitative evidence, suggests that end-series computational problems may interfere with the dendrochronological identification of temporal growth trends, especially when ring indices are computed as ratios. Whenever tree-ring data are the only source of information about past tree growth trends, it appears desirable to evaluate trends based on both ring-width series and ring-area series, and to critically evaluate the synthesis provided by the final tree-ring chronology, especially considering that prediction of future trends weights heavily the most recent portion of the historical record.
FIGURE V.1. Time-series graph of crossdated ring-width series (N = 58) from 1570 to 1990 for cored pines with 1990 DBH (a) < 50 cm, and (b) ≥ 50 cm. A dashed vertical line marks 1920, the beginning of the forest inventories.
DBH < 50 cm in 1990

(a)

DBH ≥ 50 cm in 1990

(b)
FIGURE V.2. The same as Figure 1, restricted to the 1850–1990 period.
FIGURE V.3.  Time-series graph of ring-area series (N = 58) from 1570 to 1990 for cored pines with 1990 DBH (a) < 50 cm, and (b) ≥ 50 cm. A dashed vertical line marks 1920, the beginning of the forest inventories.
FIGURE V.4. The same as Figure 3, restricted to the 1850–1990 period.
DBH < 50 cm in 1990

RING AREA
(cm²/π⁻¹)

DBH ≥ 50 cm in 1990

RING AREA
(cm²/π⁻¹)
FIGURE V.5. Time-series graph of 10-year periodic basal area increment (N = 29) derived from ring-area series of pines with 1990 DBH ≥ 50 cm.
FIGURE V.6. Time-series graph of 10-year periodic basal area increment (N = 29) derived from ring-area series of pines with 1990 DBH < 50 cm.
FIGURE V.7. Time-series graph of tree-ring chronologies derived from ring-width series of pines with 1990 DBH < 50 cm (SMALL), ≥ 50 cm (LARGE), and of all cored pines (ALL). A dashed vertical line marks year 1920. In option 0 (above) no standardization was used before averaging the normalized ring-width series. In option 1a (below), standardization included fitting a negative exponential or straight line to the ring-width series, then computing ring indices by division.
FIGURE V.8. The same as Figure 7, restricted to the 1850–1990 period.
FIGURE V.9. Time-series graph of tree-ring chronologies derived from ring-width series of pines with 1990 DBH < 50 cm (SMALL), ≥ 50 cm (LARGE), and of all cored pines (ALL). A dashed vertical line marks year 1920. Standardization included fitting a cubic spline to the ring-width series and computing ring indices by division. The cubic spline in option 1b (above) is much more flexible than that in option 1c (below).
Option 1b

Option 1c
FIGURE V.10. The same as Figure 9, restricted to the 1850–1990 period.
FIGURE V.11. Time-series graph of tree-ring chronologies derived from ring-width series of pines with 1990 DBH < 50 cm (SMALL), ≥ 50 cm (LARGE), and of all cored pines (ALL). A dashed vertical line marks year 1920. In option 2 (above) standardization included fitting a negative exponential or straight line first, and then fitting a stiff cubic spline, always computing ring indices by division. In option 3 (below) standardization included fitting a stiff cubic spline to log-transformed ring widths, and computing ring indices by subtraction.
Option 2

Option 3
FIGURE V.12. The same as Figure 11, restricted to the 1850–1990 period.
FIGURE V.13. Time-series graph of tree-ring chronologies derived from ring-width series of pines with 1990 DBH $< 50$ cm (SMALL), $\geq 50$ cm (LARGE), and of all cored pines (ALL). A dashed vertical line marks year 1920. In option 4 (above), the flexible cubic splines fitted to the ring-width series were normalized and then averaged together. In option 5 (below) no standardization was used before averaging the normalized ring-area series.
FIGURE V.14. The same as Figure 13, restricted to the 1850–1990 period.
FIGURE V.15. Time-series graph of tree-ring chronologies derived from ring-width series of pines with 1990 DBH < 50 cm (SMALL), ≥ 50 cm (LARGE), and of all cored pines (ALL). A dashed vertical line marks year 1920. In option 6 (above), standardization included first-differencing log-transformed ring widths. In option 7 (below), standardization included first- and second-differencing log-transformed ring widths.
FIGURE V.16. The same as Figure 15, restricted to the 1850–1990 period.
VI. FINAL CONSIDERATIONS

This research uncovered growth trends associated with changes in stand structure during the twentieth century in an old-growth stand of southwestern ponderosa pine (*Pinus ponderosa* Dougl. ex Laws. var. *scopulorum*). The role of climate and competition in shaping the observed trends was investigated using multiple data sets. Repeated forest inventories, dendrochronological series and daily meteorological records were available at the Gus Pearson Natural Area, a 800x400-m permanent plot maintained by the U.S. Forest Service since 1920 near Flagstaff, Arizona. Forest inventories, repeated at 10-year intervals from 1920 to 1990, showed that tree density and stand basal area increased, periodic basal area increment of the whole stand was stationary, and growth rates of individual trees declined regardless of size class (Chapter II). Temporal growth trends were quantified by size class using a mixed linear model to account for variability across trees as well as within trees. Growth of large pines, whose density increased slightly, declined more than that of small pines, whose density almost tripled. I argued that, other factors being equally important among size classes, competition for resources was more detrimental for growth rates of large trees than for those of small trees.

Pearson (1950, p. 67–68) first proposed that root competition for soil moisture with the newly established pine regeneration was responsible for the decreased growth rates of large pines. In open stands, lateral roots of southwestern ponderosa pine usually extend beyond the crown to about 70% of tree height (Schubert 1974, p. 12), hence lateral
roots of large, mature pines with an average height of 30 m may be up to 25–30 m long. In dense stands, however, laterals "probably go but little beyond the spread of the crown" (Pearson 1931, p. 93). With increased density during the twentieth century, lateral roots of large, pre-settlement ponderosa pines could have experienced dieback, hence the volume of soil exploited by fine roots could have shrunk. If root competition limits ponderosa pine growth, shorter active laterals should correspond to a reduction of distances over which inter-tree competitive interactions take place. Interestingly, spatial dependence of pine growth rates was modelled using a variogram range of 30 m (Chapter III), but even shorter ranges — e.g. 10 m — could be used to model variograms after 1920, possibly indicating a shorter spatial extent of tree-to-tree interference.

Despite increased crowding, stem size maintained the same type of spatial dependence from 1920 to 1990 (Chapter III). Geostatistical analyses showed that stem size was spatially autocorrelated over distances no greater than 30 m, a measure of average patch diameter in this forest ecosystem. Even though the variability in shape and size of pine groups could not be quantified, this average patch dimension agrees well with results of other studies on forest structure of southwestern ponderosa pine (Chapter III). The independence between patch size and time indicated that stand density increased by increasing the number of pine groups, not their horizontal dimension. Therefore, one can hypothesize that stand patchiness, in this forest type, is not only caused by fire regime, as previously thought, and is rather a function of both fire regime and the dissemination process. According to Schubert (1974, p. 43), "ponderosa pine seeds are not disseminated
far from the seed tree", and most seedfall usually falls within a distance of one to two times the tree height. Average height of the large, mature yellow pines, which produce the heaviest cone crops (Schubert 1974, p. 42), is about 30 m at the study area.

Before Euro-American settlement, fire may have enhanced the patchiness of the stand by thinning the small groups of even-aged pines that periodically became established. It is possible that only one or two trees per group survived the fire-driven thinning process. By letting only few individuals survive and reach maturity, fire perpetuated patchiness, because isolated point sources of viable seeds were left across the landscape. Moreover, if the area originally occupied by one even-aged group was largely freed by fire, it could then overlap with the area occupied by another even-aged group established some or several years later. This mechanism, repeated two or more times, would result in scattered, uneven-aged groups, hence it provides an alternative to White's (1985) hot-spot theory for explaining the age structure of pine groups at the study area.

Spatial dependence of stem size — diameter, basal area — was always much greater and decreased less through time than that of stem growth — periodic basal area increment. Spatial dependence of stem increment was close to zero in the most recent decade, indicating that growth rates in 1980-90 varied regardless of mutual tree position. Increased tree crowding corresponded to lower average, variance, and spatial dependence of individual growth rates. Since growth variation was less related to inter-tree distance at higher tree densities, density-dependent limitation of tree growth did not necessarily correspond to distance-dependent growth rates. Based on amount of spatial dependence,
prediction of individual stem sizes benefits from information on horizontal stand structure, but prediction of individual growth rates is independent of mutual tree position when stand density exceeds threshold values. Simulation models and area estimates of tree performance in old-growth forests may be improved by including geostatistical components to summarize ecological spatial dependence.

No significant trend from 1910 to 1990 was found in climatic variables computed from daily meteorological records (Chapter IV). Climate fluctuated at the decadal and yearly time scales, but the decline of individual growth rates identified in repeated forest inventories (Chapter II) and the decrease over time of spatial dependence of stem increment (Chapter III) could not be related to any long-term change in climate at the study area. Summer drought during the 1940s and 1970s may have accelerated the decline of pine outgrowth and basal area increment, and may also have heightened pine mortality. Further testing of these hypotheses could be based on the inclusion of appropriate density and climatic factors in the mixed linear model described in Chapter II.

Results of dendroclimatic analyses reported here were consistent with those obtained by other authors throughout the 1900s. This indicated that climate-tree growth relations had not significantly changed over the twentieth century. Annual growth of both large and small pines was positively related to winter snowfall and to July monsoon rainfall. Small pines showed a tendency to respond more to summer precipitation than to winter snowfall, and large pines showed a tendency to respond more to winter snowfall than to summer rainfall. However, when rigorously tested, these differences between
correlation coefficients were not statistically significant. These results support the notion that snow cover benefits tree growth by alleviating moisture stress during May and June, rather than by protecting trees from winterkill. According to Schubert (1974, p. 14), "Winterkill occurs when the soil moisture within the root zone is frozen and unavailable to the plant, while the plant continues to transpire and use water". This winter drying, which may reduce annual growth by killing pine needles, is minimized when abundant snow cover prevents soil freezing. Since winterkill affects mostly the small trees, it should produce a stronger positive winter precipitation signal in small pines than in large pines.

Precipitation signals highlighted by bootstrapped response functions could have important implications for reconstructions of ecosystem dynamics in southwestern ponderosa pine forests. Successful pine regeneration usually depends on July precipitation for seed germination (Pearson 1923, Cooper 1960, Schubert 1974). White (1985) considered May and June as the critical period for seedling survival, hence he suggested that tree-ring chronologies derived from mature pines may not yield much information on historical periods that were climatically favorable to pine regeneration. In reality, according to Pearson (1950, p. 116), "Only in 1919, during the entire period of years from 1909 to 1945, did appreciable germination take place before July in the Coconino and Kaibab National Forests", and "Even in that year, however, most of the western yellow pine seeds lay dormant until daily showers in July provided ideal conditions for growth" (Pearson 1931, p. 64). Besides the direct positive effect of July precipitation on pine
regeneration, there are indirect positive effects of winter precipitation, *i.e.* snowfall, which is the other major climatic signal identified in tree-ring chronologies. Abundant snow cover greatly reduces frost heaving and soil freezing, two important causes of mortality among pine seedlings (Schubert 1974, p. 11).

Dendroclimatic results were not completely unrelated to the endogenous transformation of site structure over the twentieth century. Variance of residuals from response functions showed a tendency to increase in the most recent decades (Chapter IV). If the climatic control of annual wood production in individual trees remained essentially unaltered, as stated in a previous paragraph, stronger deviations from the average climate-tree growth relations may be attributed to increased stand density and competitive interactions. Tree growth may have been more limited by climate than by competition during the first part of the century, but with increased crowding, the influence of climate on tree growth may have been reduced. Even though favorable climatic conditions contributed to the successful regeneration pulses that increased stand density, and that reduced the strength of climate-tree growth relations, the use of residual tree-ring chronologies computed from a large sample size is a plausible guarantee that dendroclimatic reconstructions at the yearly time scale will be independent of site conditions.

Periodic basal area increment obtained from dendrochronological data revealed that forest inventories over-estimated growth rates, especially for small pines (Chapter V). On the other hand, tree-ring chronologies developed using different standardization options showed different temporal trends during the twentieth century. Based on ring-width and
ring-area series, the establishment of the Gus Pearson Natural Area coincided with the largest peak and with the onset of the longest decline of individual tree growth in the last three centuries. Whenever tree-ring data are the only source of information about past tree growth trends, it appears desirable to evaluate trends based on both ring-width series and ring-area series, and to critically evaluate the synthesis provided by the final tree-ring chronology, especially considering that prediction of future trends heavily weights the most recent portion of the historical record. In conclusion, repeated forest inventories quantified growth rates of individual trees and of the entire stand, but DBH measurements integrated both bark and wood increment. Dendrochronological data had superior temporal resolution and accuracy, but their limited spatial coverage hindered representation of growth trends for the entire stand.

An important distinction needs to be made between trends quantified for the entire stand and trends quantified for individual trees. The former must consider the population processes of mortality and recruitment, or ingrowth, to obtain accurate results. The latter may be influenced by changes in density caused by ingrowth and mortality, but do not necessarily require accurate computation of population processes. The present study was intended to address and clarify some of these issues. For instance, a distinction was made in Chapter II between total stand density and basal area, which increased from 1920 to 1990, and basal area increment of individual trees, which decreased from 1920 to 1990. Mortality and ingrowth were essential to quantify stand performance, but were not needed to compute growth rates of individual trees, even though ingrowth most likely affected
those growth rates. Similarly, tree-ring chronologies may not accurately reflect growth
trends of the entire stand (Chapter V), but they provide extremely precise and accurate,
high-resolution data on temporal trends for individual trees as they relate to year-to-year
climatic variation (Chapter IV). Because mixed linear models allow the analysis of
temporal growth trends without assuming any specific growth curve (Chapter II), further
research should investigate the application of mixed linear models for trend detection in
tree-ring series.

Several new scientific questions and lines of research could originate from this
study. First, it would be desirable to extend trend detection to aboveground primary
productivity. Several agents may be responsible for the increase in total density and basal
area of the stand over the last decades. Given the ecology of southwestern ponderosa
pine forests, fire suppression is the most likely culprit. However, identification of
additional fingerprints, including increasing atmospheric carbon dioxide, will necessarily
be preceded by a quantitative representation of biomass increment. Aboveground dry
weight could be computed from allometric equations developed at the study area (Gholz
et al. 1979), a rare advantage in productivity studies. In these equations, stem diameter
outside bark is the only predictor of stem wood, bark, living branches, dead branches, and
total foliage biomass. Forest inventories could be used to obtain biomass values of
individual pines and of the whole stand at 10-year intervals from 1920 to 1990.

The contribution of dog-hair thickets, not included in the inventories, to
aboveground primary productivity needs to be evaluated. It would also be important to
reconstruct in finer detail the pattern of site occupation during the twentieth century. Preliminary results based on vegetation transects and dendrochronological analyses indicate that dog-hair thickets generated at different times. Extensive tree-ring analysis of age distribution and growth rates of pine clusters would provide clues as to the effect of climatic regime on successful ponderosa pine regeneration. It would also test the hypothesis that climatic variation controls year-to-year growth patterns, but it is crowding that determines mean growth rates. Ongoing restoration efforts of the Gus Pearson Natural Area include cutting post-settlement trees (Covington, pers. comm.), and the information needed for the above mentioned studies could be obtained by salvaging specimens from felled trees.

Historical information on the productivity of dog-hair thickets could be obtained from repeated aerial photographs. Aerial stereo photographs of the entire area were taken in 1984, 1978, 1967, 1959 and 1949. The 1949 and 1959 photos were in black and white, whereas the others were in color. The last (1984) and first (1949) aerial photos could be scanned, referenced against a topographic map, rectified (Jensen 1986) and imported into a GIS computer program using pixel size of 1x1 m. Supervised and un-supervised classification schemes applied to digitized images could be used to quantify ground cover by vegetation class, including large pines, small pines, pines too small to be inventoried, and non-forested areas. Furthermore, an even more accurate representation of spatial trends and patterns could be obtained by stem mapping all pines presently included in the forest inventory. Then, hypotheses on past growth rates and spatial interactions could be
tested by statistically predicting stem diameter of tagged pines in the year 2000, and checking results against the next forest inventory of the study area.

Comprehensive site histories spanning several decades are a unique tool to understand the consequences of management strategies in terms of short- and long-term availability and quality of natural resources. The methods presented in this study to assess spatial and temporal growth trends are promising, and it is now necessary to expand this multi-sided, interdisciplinary approach to larger spatial scales and different forest types. Long-term ecological research sites are ideally suited for the task, because they provide records of sufficient duration to distinguish year-to-year variation from variation at the decadal time scale. By expanding the spatial dimension of the present work it will be possible to determine under which conditions the lessons learned at the Gus Pearson Natural Area can be applied to other locations. Integration and synthesis of information across long-term ecological research sites will not only improve our understanding of ecosystem dynamics, but also provide a baseline for measuring environmental changes, and possibly evaluating the adverse impacts of human activities.
VII. REFERENCES


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