

Preliminary relationships between climate and the apical extension, needle production and ring width of *Pinus ponderosa* in Arizona, USA

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ABSTRACT

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Measurements of apical extension (height increment), needle production and ring width from a detailed sequence of measurements on one *Pinus ponderosa* tree from the Santa Catalina Mountains, southern Arizona, USA for the period 1962-1998 are presented. From these measurements the relationships between tree age and height, and tree height and diameter at breast height are determined. These are compared with the overall site trends for the same relationships determined from height and basal age of individual trees, and the site ring width chronology to test whether the growth of the individual tree is comparable with that of other trees at the study site.

Needle production and apical extension are highly correlated ($r = 0.67$) and show generally similar climate correlations. Ring widths are not significantly correlated with either of these series but all three series are significantly positively correlated with precipitation and dew point temperature during the relatively dry months of March, April and May of the growth year. This seems to be the dominant factor influencing ring width growth. However, needle production and apical extension also appear to be related to both climatological conditions during the year of bud formation as well as during the year of growth. These relationships can be explained by either bud formation processes, depletion of stored carbohydrates that would otherwise be used for bud formation or variations in the rate of apical growth. Further data are required to support some of the climate relationships.

Although there was suppression in the early growth of the individual tree, for the periods when the needle density data and isotope tracer results apply, growth of the individual tree corresponds with average site growth trends. Given this consistency, it is not unreasonable to use the needle production and stable isotope tracer results, which are only available for this tree, to calibrate, verify and parameterise the Tree Ring model.

Key-words—Needle trace method, Apical extension, Ring width, Tree ring model, *Pinus ponderosa*.

अमरीका के एरीज़ोना प्रान्त से प्राप्त पाइनस पॉन्डीरोसा की जलवायु एवं शीर्षस्थ विस्तार में सम्बन्ध, सूचिका उत्पादन एवं वलयी चौड़ाई
डेबी हेमिंग, रिस्तो जैकेनन एवं स्टीवन डब्ल्यू. लीविट

सारांश

वर्ष 1962-1998 की अवधि हेतु अमरीका के दक्षिणी एरीजोना प्रान्त के सान्ता केटेलीना पर्वतश्रेणियों से प्राप्त एक पाइनस पॉन्डीरोसा वृक्ष के अनुमापनों के विस्तृत अनुक्रम से शीर्षस्थ विस्तार (ऊँचाई में वृद्धि), सूचिका उत्पादन तथा वलयी चौड़ाई के अनुमापनों को प्रस्तुत शोध पत्र में प्रस्तुत किया गया है। इन अनुमापनों से वृक्ष ऊँचाई पर वृक्ष की आयु एवं ऊँचाई तथा वृक्ष ऊँचाई एवं व्यास के मध्य के सम्बन्धों को विश्लेषित किया गया है। अध्ययन स्थल के अन्य वृक्षों के साथ इस वृक्ष की वृद्धि तुलनीय है अथवा नहीं, यह जाँचने हेतु इनकी वृक्ष विशेष भी ऊँचाई एवं आधारीय आयु से निर्धारित किए गए, उन्हीं सम्बन्धों हेतु सम्पूर्ण स्थल रूझानों के साथ तुलना की गई।

सूचिका उत्पादन तथा शीर्षस्थ विस्तार उच्चतः सहसम्बन्धित (आर = 0.67) हैं तथा सामान्यतः एक समान जलवायुविक सहसम्बन्धन प्रदर्शित करते हैं। वलयी चौड़ाइयाँ इनमें से किसी भी श्रेणी से महत्त्वपूर्ण रूप से सहसम्बन्धित नहीं हैं, किन्तु वृद्धि वर्ष के मार्च, अप्रैल एवं मई माह के अपेक्षाकृत शुष्क महीनों के दौरान सभी तीन श्रेणियाँ वर्षण एवं ओस बिन्दु तापमान के साथ सकारात्मक रूप से अत्यन्त महत्त्वपूर्ण ढंग से सहसम्बन्धित हैं। यह वलयी चौड़ाई को प्रभावित करने हेतु सबसे प्रमुख कारक है। यद्यपि वर्ष में कली के निर्माण के दौरान तथा वर्ष में वृद्धि के दौरान दोनों जलवायुविक स्थितियों से सूचिका उत्पादन तथा शीर्षस्थ विस्तार भी सम्बन्धित प्रतीत होते हैं। इन सम्बन्धों को या तो कली निर्माण प्रक्रिया अर्थात् संरक्षित कार्बोहाइड्रेटों के हास, जिसे कली निर्माण में प्रयुक्त किया जा सकता था, अथवा शीर्षस्थ वृद्धि की दर द्वारा व्याख्यायित किया जा सकता है। कुछ जलवायुविक सम्बन्धों के समर्थन हेतु और अधिक आंकड़ों की आवश्यकता है।

यद्यपि अवधि के दौरान सूचिका घनत्व आंकड़ों तथा समस्थानिक अनुरेखक (ट्रेसर) के परिणामों को अनुप्रयुक्त करने पर वृक्ष विशेष की प्रारंभिक वृद्धि में लुप्तांगता (सप्रेशन) प्राप्त हुई है, परन्तु वृक्ष विशेष की वृद्धि औसत स्थल वृद्धि रूझानों के संगत है। इस संगति के आधार पर यह तर्कसंगत होगा कि सूचिका उत्पादन तथा स्थाई समस्थानिक अनुरेखक के परिणामों को प्रयुक्त किया जाए, जो मात्र इस वृक्ष के वृक्ष वलय प्रतिदर्श के अनुसंशोधन, अभिप्रमाणन तथा प्राचलीकरण हेतु ही उपलब्ध हैं।

संकेत शब्द—सूचिका अनुरेखक प्रविधि, शीर्षस्थ विस्तार, वलयी चौड़ाई, वृक्ष वलय प्रतिदर्श, पाइनस पॉन्डीरोसा.

INTRODUCTION

THE Tree Ring model (Fritts *et al.*, 1999) is a process model that uses daily climatological inputs to estimate various tree functions, including cambial activity and isotopic fractionation. Throughout the development of the Tree Ring model it has been vital to parameterise, calibrate and verify the model with real measurements that are representative of the species and study site that is being modelled. At present, this is done using *Pinus ponderosa* (Ponderosa pine) in the Santa Catalina Mountains of southern Arizona, USA.

For some variables such as ring width and tree height to age relationship, it has been possible to sample and average a representative cross-section of the tree population at the study site. However, for other variables this has not been possible, either because the measurements are destructive or too time consuming to be feasible to measure on more than one or a few trees. In this situation we aim to justify using data that is only available from one or a few trees to provide inputs for the Tree Ring model by checking that the growth of this tree is comparable with that of site averages and consistent with expected climate relationships.

Time series derived from apical extension and ring width for the individual tree in this study are compared with site average curves and, together with time series of needle production, these are compared with climate parameters. If the growth of this tree is shown to be site-consistent, information on photosynthetic allocation from an isotopic tracer experiment conducted on this tree could also be used to verify the modelling of the intra-annual timing of cell development and isotopic composition.

METHODS

An individual ponderosa pine tree from a study site in the Santa Catalina Mountains of southern Arizona, USA (32°42'N, 110°75'W) was felled in February 1999 as part of an isotopic tracer experiment designed to examine the timing of tree ring cell development. This tree was utilised for the present study because sufficient tree material was available for the destructive needle trace density determination.

To check that the growth of the individual tree was indicative of the growth of other trees at the study site a ring width chronology, age versus height curve and height versus diameter at breast height (dbh) curve were constructed using

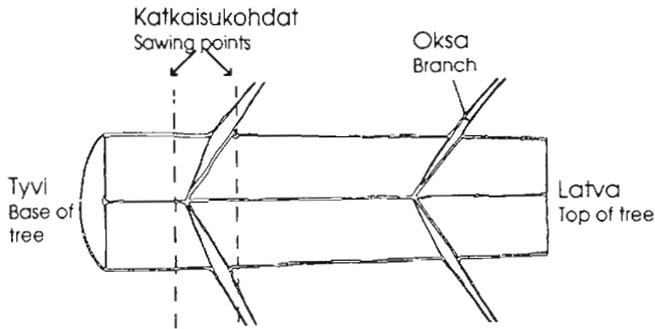


Fig. 1—Sectioning annual branch whorls (After Aalto & Jalkanen 1998)

multiple trees from the site. These were compared with the same measurements made on the individual tree.

Apical Extension and Tree Height

A time series of apical extension was determined on the individual tree by sectioning and measuring the distance between annual branch whorls (Fig. 1), and associating each section with the relevant year of formation and age of pith. By cumulating these apical extension measurements a time series of tree height versus age was also obtained. This individual tree series was compared with a tree height versus age curve for a cross-section of ponderosa pine at the site, which was determined using two techniques:

- On young trees where annual branch whorls are clearly visible tree age was determined by counting branch whorls from the base. Height was determined with a tape measure.
- On older trees or where all branch whorls were not clear, measurements of tree age (at coring height ~1.5 m)

were estimated from tree cores by adding 20 years to this pith age. Height measurements to the highest visible shoot were made using a clinometer and triangulation.

Needle Production

The Needle Trace Method (Aalto & Jalkanen, 1998; Jalkanen *et al.*, 1998) was used to determine the number of needles that grew on each new apical growth section in each year from 1962 to 1998. This is referred to as needle production. From each of these sections a rectangle of wood approximately 5 cm long was taken surrounding the pith. Using a sharp blade, shavings of wood were removed around the circumference of the pith until a bolt of wood containing the inner-most ring was reached.

As the vascular bundle connecting each dwarf shoot to the new apical stem extends to the pith, and its location is identified after needle shed by a 'scar' (a needle trace), the number of needle traces on the inner-most apical growth ring indicates needle production for that year. To determine needle production the number of needle traces on each bolt was divided by the bolt length to get needle density (needles per unit of apical growth), which was multiplied by length of apical growth.

As with other pine species, ponderosa pine grows needles around the stele at set intervals along a spiral route. If a needle trace seemed to be missing from this spiral further slivers of wood were removed from the section until the trace was exposed.

Ring Widths and DBH

To produce the individual tree ring width series, ring widths were measured on two sides of a disk taken from

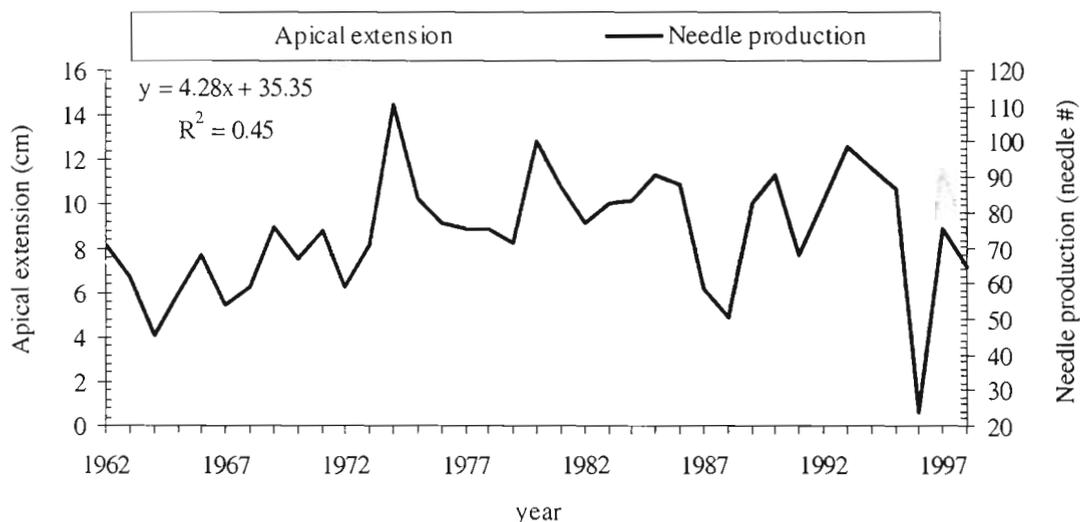


Fig. 2—Time series of apical extension and needle production for a *Pinus ponderosa* in the Santa Catalina Mountains, Arizona, USA.

approximately 1.5 m height. These were averaged to produce a raw ring width series, then an indexed series was produced using a 50 years spline with a 50% cut-off wavelength. The diameter of this disk was assumed to correspond to dbh. A time series of dbh versus height for the tree was constructed by subtracting the cumulative diameter added by each consecutive average raw ring width from this initial dbh measurement and comparing this with the corresponding height measurements. This individual time series is compared with the site series for dbh versus height that was constructed by measuring the dbh of the same trees used to determine the height versus age curve.

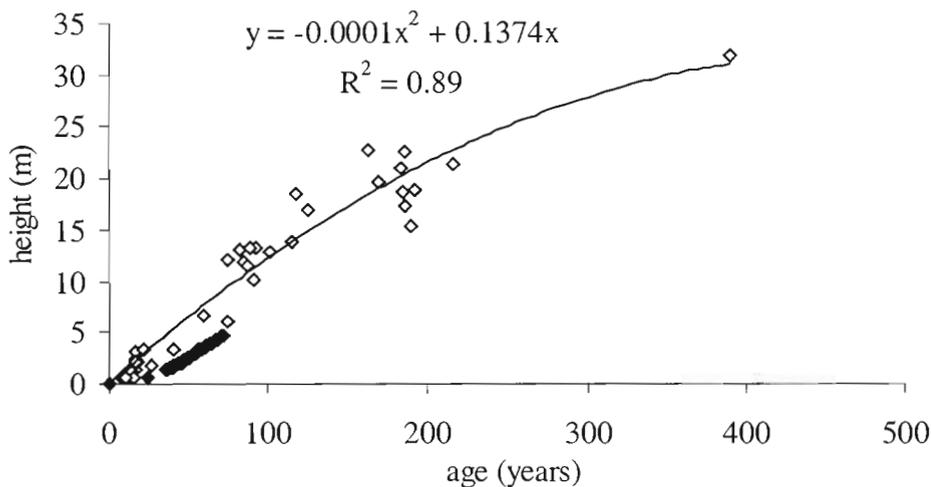
The site ring width chronology was constructed by averaging the ring width series of four perpendicular cores from each of nine trees, all between 55 and 133 years old. The resultant series were then indexed, again using 50-years

splines with a 50% cut-off wavelength prior to being averaged to form a single chronology.

Climate comparisons

The relationships between the tree growth time series and monthly average climatic parameters are examined by cross-correlation analysis using the monthly climate parameters for the same year and for the year prior to tree growth. The climate parameters used are average, maximum and minimum temperature, precipitation and dew point temperature. For the period 1965 to 1981 the temperature and precipitation records were directly available from the Palisades Meteorological Station, which is approximately 1 km from the study site. Some missing values in this record were reconstructed using regression relationships between the

a) Tree height Vs age



b) Tree height Vs dbh

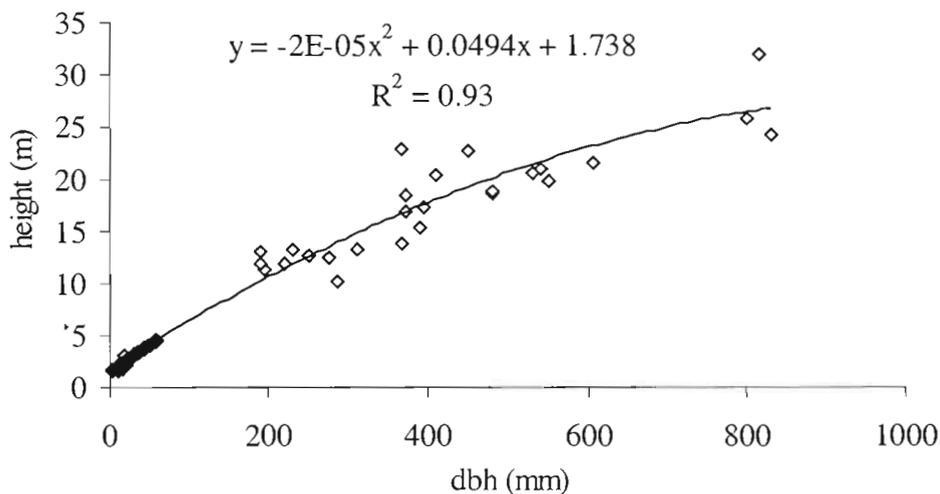


Fig. 3—Relationship between (a) tree height and age and (b) tree height and dbh. The single 'tracer' tree is shown by filled diamonds and the observations from multiple trees at the site are shown by open diamonds. A first-order polynomial is fitted to the multiple tree site data only.

available Palisade data and records from a network of five meteorological stations within a site radius of 25 km.

RESULTS AND DISCUSSION

Tree Measurements

For the individual tree there is a highly significant positive correlation ($r=0.67$, $p<0.001$) between apical growth and needle production (Fig. 2), but no significant correlation between these series and ring width (raw or indexed). This indicates that the factors, and possibly the timing of factors, influencing apical extension and needle number are similar, but these are different to those factors affecting ring width growth. Poor or non-significant correlations between ring width and apical extension or needle number have also been observed on *Pinus sylvestris* in Finland (Jalkanen, In prep.), and attributed to differences in the time window of climatological influence (Jalkanen, 2000). This is discussed further in the following section.

The relationship between the site curves for height versus age and height versus dbh compared to those for the individual tree are shown in Fig. 3a and b respectively. It is evident from the curve of height versus age (Fig. 3a) that the apical growth of the individual tree was relatively suppressed compared to trees of comparable age in the same stand. The main period of suppression occurred in the first thirty years of growth, until approximately 1960, after which the slope of the height to age curve is nearly parallel with that of the site average, indicating that after initial suppression growth continued at a rate comparable with the site average. This is supported by the close association between the individual tree and the site average curves for height versus dbh (Fig. 3b), which is unaffected by suppressed growth in the individual tree because the height at which dbh is taken (~1.5 m) was not reached until after 1960. The indexed ring width series is highly correlated with a site ring width chronology ($r=0.62$, $p<0.001$), also indicating that the inter-annual growth of this tree was similar to the site average.

As the isotope tracer experiment was completed in 1998 growth during this period is also outside the period of suppression and appears to be comparable with site averages. It should therefore be reasonable to assume the isotopic responses are similar to those expected from other comparable trees at the site.

Climate and Tree Measurements

Comparing the series of apical extension, needle production and ring width with climatic parameters (Fig. 4), apical extension and needle production are most significantly

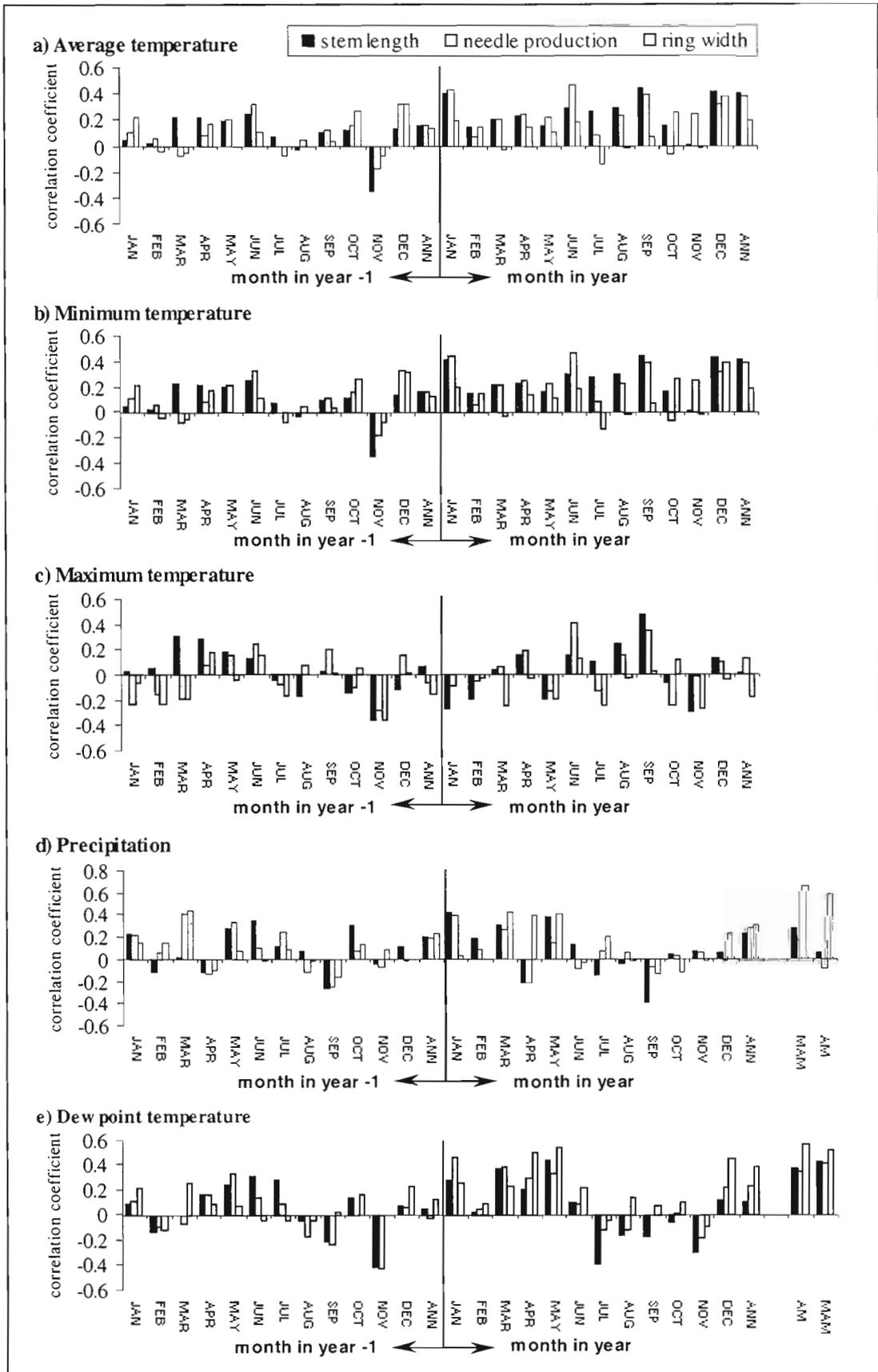
correlated with similar climatic parameters and time periods, but these are often different from those most significantly correlated with ring width.

One period when all three tree series are significantly correlated with climate is with precipitation and dew point temperature is during spring (March-May) of the growth year (Fig. 4d & e). This is associated with the initial growth flush in the shoots, needles and stem, and is in agreement with observations of approximately coincident timing between initial height increment and stem diameter growth for *Pinus ponderosa* grown over a two year period in open-top field exposure chambers in California, USA (Tingey *et al.*, 1996). The fact that temperature during this time period does not show significant relationships with any of the tree series suggests that initiation of inter-annual growth is influenced more by moisture availability than temperature. This is supported by the observations that soil moisture is the factor most limiting to growth throughout the geographical range of *Pinus ponderosa* (Burns & Honkala, 1990), and ring widths of this species growing in arid US sites were more dependent on spring precipitation than temperature (Fritts, 1976 p. 240).

Apical extension and needle production are also significantly positively correlated with average and minimum temperature in January and during several of the summer months. As January precipitation is also significantly correlated with these series this relationship may be explained by the amount of winter snow-pack available for initial spring growth. However, the correlations with summer temperature do not seem to be well explained physiologically. It is possible that further smaller growth flushes occur in apical extension throughout the summer, as was observed by Tingey and others (1996) for ponderosa pine however, more observations are required to support this relationship.

Climate variables between the months of March and June of the previous year are generally positively correlated (not always significantly) with both stem extension and needle production. This is the period prior to the initiation of the summer monsoon (which is between early July and October) when stored carbohydrates may be significantly depleted. If conditions are favourable for growth during this time less stored carbohydrate will be depleted and more will therefore be available for bud preparation later that year.

It is also notable that there is a significant negative correlation between November climate (except precipitation) and both stem extension and needle production. This relationship was also noticed for *Pinus sylvestris* in Finland, but for the November two years prior to growth (Jalkanen, 1999; McCarroll & Jalkanen, 1999). It is possible that warm and humid November conditions increase respiration over photosynthesis in ponderosa pine at this location, which will again tend to reduce the carbohydrates available for growth the following season.



CONCLUSIONS

Although growth was initially suppressed in the individual tree, during the period 1962 to 1998 it is comparable to that of other trees at the same site. Although not an ideal situation, this justifies the use of data that are only available from this tree during this time period (needle density and isotopic tracer results) for calibration, verification and parameterisation of the Tree Ring model.

Needle production and apical extension are highly positively correlated, indicating that similar factors influence these two variables. However, these factors must be different from those affecting ring width because ring width is not significantly correlated with these series.

Spring moisture during the year of growth is significantly correlated with all three tree series and is the factor most dominant for ring width growth. However, climate relationships with apical extension and needle production appear to be more complex and are related to both climatological conditions during the year of bud formation as well as during the year of growth. These relationships can be explained by either bud formation processes, depletion of stored carbohydrates that would otherwise be used for bud formation or variations in the rate of apical growth.

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Fig. 4—Correlations between climate parameters and apical extension, needle production and ring width for the individual tree. Monthly average climate parameters of (a) average temperature, (b) minimum temperature, (c) maximum temperature, (d) precipitation, & (e) dew point temperature for the year of growth and prior year have been used. Abbreviations of MAM and AM have been used to signify averages for March-May and April-May. Correlations of ± 0.34 and better are significant at the 95% level.