How well understood are the processes that create dendroclimatic records?
A mechanistic model of the climatic control on conifer tree-ring growth dynamics

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Abstract

We develop the observational and conceptual basis for modeling conifer cambial processes as a direct but nonlinear and multivariate response to external environmental conditions. The model, here termed Vaganov-Shashkin (VS), reproduces the critical features linking climate variability to tree-ring proxy formation. We discuss recent test simulations of tree-ring width data from a variety of sites and spatiotemporal scales. Our experiments demonstrate that the model skillfully reproduces observed patterns of tree-ring growth across a range of environments, species, and scales. Model performance is found to be robust to parameter estimation. We discuss present and future applications of the VS model, including exploration of the biological basis of emergent phenomenon and prediction of the influence of climate change on conifer tree growth dynamics.

Introduction

Climatic variation is a major factor affecting tree ring growth and wood formation. Accordingly, there has been a significant amount of dendroclimatology research focused on the extraction and validation of climatic variability from tree ring data series (Fritts 1966; Cook and Jacoby 1977; Fritts et al. 1979; Hughes et al., 1984; more recently, see for example Stahle and Cleaveland 1992; Grissino-Mayer 1996; Villalba et al. 1998; Briffa et al. 2001, 2004; Cook et al. 2002; Pederson et al. 2004; Watson and Luckman 2004; Salzer and Kipfmueller 2005). The main morphological and anatomical characteristics of tree rings bearing the climatic signal have been described: tree ring width, density profile, cell diameter, and cell wall thickness (Vaganov 1996). Although stable isotope methods and models are increasingly valuable (McCarroll and Loader 2004), the most widely-used tree ring characteristics for climate reconstructions have been tree ring width and maximum latewood density. Such reconstructions have relied almost entirely on statistical covariation of the proxy observations and climate data during the modern period.

But H.C. Fritts saw the vital importance of concurrent research into the anatomical pattern of tree ring formation in response to changing environment. He was one of the first to make a careful

study of tree ring formation in ponderosa pine on the anatomical level, showing how the current and previous weather conditions affect the seasonal growth and cell dimensions of tree rings (Fritts 1966; Fritts 1976). Studies like this have provided broad knowledge about which processes in the growing tree control cell production and which determine the characteristics of those cells which are produced. Briefly, tree ring formation occurs in the active vegetation season, and the processes involved in tree ring formation integrate the previous and current seasonal conditions. Growth starts with cambial zone activation (activation of the fast divisions of cells). Newly produced cells progress to enlargement, and finally to cell wall thickening. At this stage the cell loses the protoplast and transforms to the "dead" element of the water conductive system of the tree.

The focus of much anatomical research since Fritts' early work has been on cambial activity (the workings of the "cambial machine"). Detailed observations and analyses of basic processes of wood formation allowed Wilson and Howard (1968, 1972, 1973) to offer a "mimic" model for the quantitative description of tree ring formation. While this model reproduced the structures formed in the tree stem during the growing season, it required an enormous number of variables and seasonal observational data that had to be specifically defined for any particular tree ring. Furthermore, the model did not include external environmental parameters. Despite the lack of explicit modeling of the external environmental influence on the processes of tree ring growth, or perhaps because of it, the nature of the environmental control of wood formation has often simply been assumed. The implicit hypothesis has been that environmental factors influence tree ring formation indirectly, through hormone and substrate balance produced by the apical meristems of shoots, and probably roots (Larson 1964; Denne and Dodd 1981).

More recently, explicit models of the link from environmental conditions to tree-ring characteristics have been developed. Perhaps the most complete of these models (albeit still considered overly simplistic by Fritts), incorporating processes linking environmental conditions to tree-ring characteristics via photosynthesis, respiration, carbon storage, and cambial processes, is TREERING2000 (a description of the fundamental model components is given in Fritts et al. 1999). This model was developed and refined exhaustively using, in part, tree-ring data and meteorological observations from the Santa Catalina Mountains in southern Arizona. Such models provide explicit tests of our understanding of the processes governing tree-ring formation and variation, and are a critical component of the science of dendrochronology.

For dendroclimatology, it would be desirable to create a tractable forward model that mechanistically includes only the critical processes which link climate variables to tree-ring formation, but whose application worldwide is not sensitive to the choice of a limited set of tunable parameters.   Such a class of models can be used to validate statistically-based reconstructions of local climate variations, the assumptions behind which may not always be valid (Cook and Pederson, 2006, this volume). For example, such models could predict a change in the dominant environmental influence on tree-ring width variations, which can be compared against actual observations. Such phenomena can only be diagnosed from *ad hoc* statistical analyses, and Cook and Pederson (2006) caution against *a priori* interpretation of tree-ring data when statistical uncertainty and emergent behavior cannot be distinguished from one another.

Here, we introduce and briefly detail the processes that control ring development in the context of the seasonal kinetics of cambial activity. We discuss the mechanisms and controls on the production, expansion, and maturation of xylem cells, and show how these may be externally influenced by climate. A mechanistic tree-ring model which integrates the primary environmental controls on conifer cambial activity is described, and we provide examples of its application in dendroclimatology. This model, here referred to as Vaganov-Shashkin (VS), also forms the cambial simulation portion of the more complete TREERING model of conifer tree growth (Fritts et al. 1999). We review recent applications of the VS model to the interpretation of tree-ring observations in a number of regions, environments, and climate change scenarios. Implicit in this review is the assumption that the VS model includes the most important processes required to successfully simulate observed characteristics of tree rings, if it can be shown that the simulations are consistent with observations. Finally, we discuss the role of forward models in the development, calibration and interpretation of tree-ring-based estimates of climate variability and change.

Cambial activity

The formation of mature xylem cells is usually considered as a process that occurs in three stages: the division of cells, the growth of cells by radial expansion and the maturation of tracheids, when cell walls thicken and the protoplast is autolysed. All stages are divided in space and in time, although they may overlap partially (Gamaley 1972). In the majority of plants, xylem is a complex tissue consisting of differentiated cells of more than one type, generated by a secondary meristem, the cambium. Plant meristems and cambium in particular, by virtue of its accessibility, became a subject of research with the appearance of the first microscope. The history of cambium research is well described, for example, in Larson's book (1994). However,

until now our knowledge of the factors initiating and regulating the origin of tissue from meristems and the physiology of meristem has been rather fragmentary. This has led to the absence of a uniform nomenclature (Catesson 1984; Schmid 1976; Wilson 1966; Larson 1994).

Cambium has common features intrinsic to all meristematic tissues and has, as a highly specialized secondary meristem, specific features:

1. It is a self-sustaining cell-like system; that is, it retains its various functions for extended periods of time, frequently throughout the life of the plant; which may last centuries or millennia;
2. In woody plants the cambium grows at the expense of the growth of the tree. An increase in the number of cambial cells happens at the expense of the division and differentiation of those cells and of the primary (apical) meristem;
3. Cambial derivatives can be differentiated into various types of xylem and phloem cells;
4. Cambium has a strictly ordered spatial organization.

The cambial cells form a continuous layer, covering the trunk, branches and roots. Therefore the cambium, on the one hand, is distributed in space, and, on the other hand, it is a linked system, where the adjacent cells are in direct contact. The spatial organization of the cambial zone is important from the point of view of regulation of its activity, as it imposes a number of specific requirements on regulation and control. Another, but not less significant, aspect of the spatial organization of the cambium is that it is the basis of the spatial cell-like organization of xylem and phloem. For example, it orders the radial tracheid files, the formation of the vessel system, and so on.

The growth of a tree ring is the result of periclinal divisions of cells in the cambial zone and of their differentiation. The growth rate depends on the number of cells in the cambial zone and their rate of division. In coniferous species, the growth of a tree ring during a season is always accompanied by a change in the number of cambial cells, which has characteristic dynamics that are general for all species (Kutscha et al. 1975; Wilson 1966; Gregory 1971; Skene 1972; Vaganov et al. 1985). In dormancy, the size of the cambial zone reaches a minimum and usually includes 4-5 cells but can reach up to 10 (Larson 1994). The radial diameter of cells in the cambial zone is equal to 5-6 μm in average but does not exceed 10 μm (Bannan 1955; Alfieri and Evert 1968; Vaganov et al. 1985). Activation of the cambial zone starts with a swelling of cells, and then the first divisions appear. After activation the size of the cambial zone is increased, and the number of cells in it increases and reaches maximum values up to 20 (15-16

on average for different species) (Larson 1994). There is evidence for a relationship between the number of cells in the cambial zone during the dormant period (and at the starting date) and the total annual production of xylem. So, Gregory (1971) found that this relationship for Alaskan white spruce is described as $N_{camb} = 3.82 + 0.05*N$ ($R^2 = 0.75$; n=37; p<0.001). Sviderskaya (1999) obtained similar results from seasonal observations of tree-ring formation in Scots pine (*P.sylvestris*) and Siberian fir (*Abies sibirica*) in the Siberian taiga (**Figure 1**).

All the available data on the duration of the cell cycle, as well as of separate phases of it, show significant variability between samples taken in different parts of a tree during a growing season, especially for the size of cambial zone. This essential variability is determined by the weather conditions of the season and other factors. Thus it is clear that the length of the cell cycle in the cambial zone changes during the growth season. Combining this statement with the observed curvilinear relationship between the number of cells in the cambial zone and annual xylem increment, we are led to the following conclusion: the regulation of cell production by the cambial zone can be achieved by increasing the number of cells in the cambial zone as well as by increasing the rate of cell division in the cambial zone.

We can summarize the results concerning the kinetics parameters of cambial activity in xylem cell production observed in different conifer species:

1. The number of cambial cells in dormant cambium and active cambium is rather different. There is a significant relationship between the number of dormant cells in the cambial zone and subsequent annual xylem increment (Skene 1972; Sviderskaya 1999).
2. The number of cells in the cambial zone varies during a season due to internal and external factors (**Figure 1**). The average duration of the cell cycle in the cambial zone varies during a season. Usually the cycle is shorter when early wood cells form and longer during formation of latewood cells, especially at the end of the growing season.
3. The total annual xylem cell production is closely related to the number of cells in the cambial zone. There is, however, a curvilinear relationship between the cell number of annual xylem increment and the average cambial cell number (Skene 1972) or the maximum cell number in the cambial zone (Vaganov et al. 1985; Sviderskaya 1999). This relationship indicates that a low rate of cell production during a season is supported mainly by an increase of the cambial zone (more xylem mother cells), but a higher rate of cell production during a season must also be associated with an increase in the rate of cell division or faster cycling of xylem mother cells.

4. There is a typical distribution of measured mitotic index along the cambial zone: moving inward from the last phloem cells produced, the mitotic index increases to a maximum approximately on third the distance across the cambial zone and then decreases, either slowly or rapidly depending on whether the cambial zone is wide or narrow (that is, depending on the number of cells in the cambial zone) (Bannan 1957; Wilson 1964).

5. There are differences in the rates of cell production even if the relationship between the number of cells produced during a season and the number of cells in cambial zone is the same (Gregory and Wilson 1968). These differences are associated with higher or lower mitotic index.

6. In conifers, the first cell divisions (in the growing season) are evident in cambial cells near to or often adjoining the last differentiated tracheids of the previous year's growth ring (Bannan 1955, 1962; Grillos and Smith 1959; Zimmermann and Brown 1971; Savidge 1993).

What can we say about the possible control of each characteristic? One possibility is that the specific growth rate distribution within the cambial zone depends on tree species as well as the geographical zone of growth (regional climate). There is some evidence for this from observations (Gregory and Wilson 1968; Sviderskaya 1999). From the dendrochronological point of view, these characteristics are more or less stable through a long period of growth and do not affect interannual variations of cell production. The dormant and especially the starting size of the cambial zone may be closely related to the previous growth and tree vigor (Dodd and Fox 1990; Sviderskaya 1999). Dendroclimatic analysis based on "cell chronologies" of larch and spruce near the northern timber line shows the significant effect of starting conditions (temperature and soil melting) on production of cells and tree-ring width (Hughes et al. 1999; Vaganov et al. 1999). These characteristics affect the interannual variability in tree-ring width and cell production. However, the starting number of cells in the cambial zone may also be affected by growth conditions in the previous year and, so, might be responsible for autocorrelation in tree-ring series that appear, at first sight, to have no climate cause (Fritts 1976). The main possible environmental control is related to intra-seasonal variations of size of the cambial zone and the specific growth rate of xylem mother cells. This thesis is supported by practically all experimental data, which show close correlation between average and maximal size of the cambial zone and annual xylem increment (see Wilson 1964; Gregory 1971; Skene 1972; Vaganov et al. 1985). In combination with cell cycle distribution across the cambial zone, these seasonal variations may explain much of interannual deviation in total cell production and tree-ring width.

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Analysis of the data shows that there are two determinants of variability in the sizes of the cambial zone: One which is more or less constant over many years, determined by the condition of the tree as a whole (growth class, vigor, energy of growth, age, position in stand etc.); and a second, an intraseasonal component, which is determined by change of the specific growth rate of xylem mother cells and on which their number also simultaneously depends (Vaganov 1996b). The first determinant can be considered as a constant on the long-term scale of the life span of a tree (some years, some decades), the second depends on current environments (climatic conditions within a season).

The assumption that the cell cycle is equal along the cambial zone throughout the season leads to the following conclusion: in order to control division it is necessary to control the size (or width) of the cambial zone (the number of dividing cells) and their specific growth rate. This means that two mechanisms are involved in control. One is clearly positional, and the other may have dependence on concentration or have some other nature. Formally, the unequal (and, in the case of the hypothesis presented here, increased) cell growth rate across the cambial zone needs only one control – positional, which is easily described in mathematical terms and the corresponding equations. Of course, nature does not always conform to the simplicity of its mathematical description.

Cell expansion

Expansion of the radial size of cells after they leave the cambial zone is the next main stage of the cytodifferentiation of xylem (Gamaley 1972; Roberts 1976). Roberts (1976) noted that at this stage "the cells exhibit high variability in the extent and regulation of expansion. The deposition of primary wall material during expansion requires the synthesis of primary wall monomers. Protein synthesis occurs. DNA replication involving endoreplication and gene amplification may occur" (Roberts 1976: 36-37). The visible result of the enlargement is greatly increased radial cell size. In early wood the radial dimension of tracheids reaches 50-60 μm; in latewood it is about 15-25 μm. So, during the formation of early wood the radial size of tracheids increases up to 7-8 times, in latewood - up to 2-3 times in comparison with the starting size of a cell in a cambial zone, which is about 7-8 μm on the average.

Most experimental results indicate that final tracheid size is not determined by the rate of radial expansion (Wodzicki 1971 Skene 1972;Vaganov et al. 1985; Dodd and Fox 1990; Sviderskaya 1999; but see Antonova et al. 1993), thus we must look elsewhere. It is obvious, however, that

such a search must focus on the period prior to radial cell expansion, namely on cell production. Sviderskaya (1999) estimated the specific growth rate of cells within the cambial zone using cell production data and the size of the cambial zone over the course of the growing season (**Figure 1**). A good relationship was found between the intraseasonal changes in the specific growth rate and changes in the size of tracheids leaving the cambium with a given growth rate. This means that the radial tracheid dimension is primarily determined by the average radial growth rate in the cambial zone or by the average rate of cell division within the cambial zone. In other words, radial tracheid dimension corresponds to the magnitude of cell production in the cambial zone.

Summarizing published data on the variability of radial tracheid dimension within conifer tree rings, we can say (Vaganov 1996a):

1. Radial tracheid dimension shows a clear seasonal trend (from earlywood to latewood) except in some subtropical and tropical trees (Vaganov et al. 1985).
2. Radial tracheid dimension shows variability due to climatic factors operating within a growing season that combines with the seasonal trend (a typical example of this is the formation of "false" rings caused by intra-seasonal drought) (Fritts 1976; Schweingruber 1988, 1996).
3. The average radial tracheid dimension is more or less constant over a long period of tree growth. These results in the close linear relationship between tree-ring width and the number of cells produced annually (Gregory 1971; Vaganov et al. 1985, 1992).
4. The range of variation in radial tracheid dimension in tree rings of different conifer species is usually limited - from 8 to 70 μm (Vaganov et al. 1985).

What indirect data confirm the suggestion that the final radial tracheid dimension cannot be effectively controlled by external influences during enlargement? They come mainly from measurements of tracheidograms (Vaganov et al. 1985, 1992). Narrow layers including only 2-3 tracheids with small radial dimension and thin cell walls can often be observed in wide tree rings from dry conditions (Fritts 1976; Shashkin and Vaganov 1993). The appearance of those cells in the earlywood zone may, in most cases, be the result of periods of moisture deficit only lasting from several days to a very few weeks. Obviously, the existence of such a layer of small, thin-walled cells cannot be due to the effect of water stress on cells that were enlarging at that time. On the other hand, if water stress affects the cells that have only just started to enlarge, then why are the other cells in the enlargement zone not affected?

There are several lines of evidence that apparently conflict with the idea that the environmental control of the final radial dimension achieved by a tracheid acts on the enlargement stage. It is, however, possible to explain this evidence if this control acts on cell production, that is, it is effective in the cambial zone, not in the enlargement zone. The evidence for the relationship between the growth rate of cambial cells and the final radial dimension of the tracheids they produce is obtained by means of a kinetic approach. It needs to be tested by other direct and indirect sets of data, because not all the questions that arise have been answered. Most questions come from the enormous volume of research on hormonal control of wood formation (see Zimmermann 1964; Barnett 1981; Creber and Chaloner 1984; Savidge 1996; Kozlowski and Pallardy 1997). There are many examples of specific and non-specific effects of hormones (auxin, IAA, gibberellin, ethylene and others) on the production rate of tracheids as well as on their size. Some of this work is based on saplings, and may be of limited applicability to mature trees in natural stands. Furthermore, we do not believe these data are necessarily contradictory to the statements made above.

We do not know the precise mechanism by which the kinetics of cell production and growth in the cambial zone determine the ultimate radial dimension of a tracheid. Recent work on root development may, however, indicate the kinds of mechanisms that may be involved. Baluska et al. (1994, 1996, 2001) hypothesized and substantiated the existence in growing roots of a so-called "transition zone" between the root meristem and the elongation zone. The main significance of this "transition zone" is as a sensory zone of the root that monitors diverse environmental parameters and effects appropriate responses (Baluska et al. 1996, 2001). For example, gravistimulation significantly changes the distribution of the relative elemental growth rate pattern along the growing root (Mullen et al. 1998). The real mechanisms are still unclear. Perhaps they operate through interactions of the gene expression responsible for the control of coordinated growth processes with hormones and growth regulators (Baluska et al. 2001; Savidge 2000). For our purposes the definition of such a special zone is very likely. This is because the results we have presented here lead us to expect the existence of some specific mechanisms of external control of cell production and enlargement at the edge of the cambial zone. We can only hypothesize that such mechanisms are related to growth rate and "movement" of cells through the cell cycle, especially through the G_1-phase. These mechanisms would provide the link between growth rate near the edge of the cambial zone and further radial enlargement. Using a simplified scheme (i.e. that the division rate at the edge of the cambial zone controls the ultimate radial diameter of the tracheid) clarifies the positional control of cell growth within the cambial and enlargement zones. Both zones (dividing cells and enlargement)

are characterized by a high rate of primary wall expansion (elongation), although the second stage has a higher rate of linear growth.

The importance of auxin in this process is clear (Rayle and Cleland 1992; Casgrove 1993; Brett and Waldron 1996). Precise determinations of gradients of IAA distribution within growing xylem and phloem show that IAA can be the hormonal signal for positional control of cell growth (Uggla et al. 1996, 1998, 2001). The results clearly indicate that IAA concentration is higher within the cambial zone with dividing cells and decreases to zero at the end of the zone of enlargement (Uggla et al. 1996, 1998, 2001). We have not here entered the discussion of the origin and maintenance of a constant level or the total value of IAA (is its control external, from the shoot -- or internal, from the cambial zone itself?). Such a picture of the distribution of one of the main hormones that is closely related to cell wall growth and cell growth regulation supports some of the assumptions we have made in a way we cannot get from direct evidence. Uggla et al. (2001) describe graphically the generalized distribution pattern of IAA, carbohydrates, and Suc-metabolizing enzyme activities across the cambial zone, zones of enlargement and maturation. If we compare the measured concentration of IAA from experiments by Uggla et al. (1996, 1998, 2001) and specific growth rate from our evaluations, we see that the maximal linear extension growth rate of cells in the enlargement zone coincides with decreasing IAA concentration (Uggla et al. 2001: Fig.1). The sucrose concentration decreases in the same direction, and SuSy activity increases in the enlargement zone and falls during cell wall thickening. All the main processes involved in the radial growth of developing tracheids, as well as in the formation of the secondary wall, are coordinated by the position of the cell in the file. The simplest explanation for the IAA pattern is that the expanding cells that have left the cambial zone use up the amount of IAA produced within the cambial zone by the dividing cells. This implies that IAA mediates the positioning signal from the cambial zone to the enlargement zone. IAA is also under the higher level control of the shoot (and root) meristems, and so it can be the mediator of the external control of cell growth within the cambial and enlargement zones. The main differences between earlywood and latewood formation are related to seasonal changes in illumination, temperature and water supply, so changes in hormone gradients between the early and later parts of the growing season indirectly show the results of environmental control of wood formation, although the main patterns remain largely similar through the season (Uggla et al. 2001, Figure 5). Quantitative variations are primarily related to the width of the cambial zone and the position of cells. This indirectly supports the hypothesis defining xylem formation as a partially independent system after the external signal from higher levels of regulation has been accepted.

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Cell wall thickening

The last stage of differentiation of the xylem elements that form the water-lifting system of the plant is characterized by completion of a rigid secondary wall with the consequent autolysis of the protoplasm. The secondary wall contains cellulose microfibrils, xylan, protein and lignin. They provide a strictly ordered structure on the exterior of the cell membrane. The three main layers in the secondary wall are distinguished by the orientation of cellulose microfibrils (Preston 1974). First there is S1, then a main, much thicker layer, S2, in which cellulose microfibrils are oriented along the axis of the cell and will frequently display spiral structures. Then comes S3, a layer that is absent in compression wood. The completion of the secondary wall involves a complex of intracellular processes and systems: the endomembrane system for transport, specialization of certain areas of the cytoplasmic diaphragm and elements of the cytoskeleton, expression of new genes, activation of numerous enzymes, and biophysical processes connected to between-cell gradients, properties of membranes and organization of the cell wall (Catesson 1994; Fukuda 1994; Demura and Fukuda 1994; Savidge 1996).

The completion of the secondary wall with its consequent lignification can be considered as the final stage in the biogenesis of the cell wall, which happens continuously during the closing stage of tracheid differentiation. Actually, the tangential and radial walls of cambial cells represent two levels of the process of maturation of primary cell walls (Catesson 1990, 1994). Tangential walls have a more rigid polysaccharide matrix in comparison with radial walls, the chemical composition and ultrastructure of which arises from the mechanical properties radial walls need for subsequent radial growth (Catesson and Roland 1981; Roland 1978). The initial heterogeneity of cambial cell walls disappears during the first stage of tracheid maturation, when the radial growth of cells is completed. It is supposed that the ratio of synthetic rates of different types of polysaccharide and their selective inclusion in radial and tangential walls predetermines the fate of the cells (Catesson 1990, 1994). For example, the earlier beginning and fast rate of xylan synthesis, mainly included in radial walls, can increase radial growth and result in formation of large tracheids or vessels. On the contrary, the synthesis of cellulose reduces an initial non-uniformity of the wall and so hinders radial growth (Catesson 1990, 1994).

All mature xylem elements (except parenchyma cells) have a thick secondary cell wall. However, thickness can noticeably differ in tracheids formed at different times in the growth season. In earlywood tracheids the cell wall is noticeably thinner (1.5 -3.0 μm). In latewood tracheids cell wall thickness can reach 7-8 μm. As well as tracheid sizes, the thickness of a cell wall can vary greatly, especially in latewood cells in various tree rings, and also in various parts

of the tree (Zahner 1968; Larson 1969; Creber and Chaloner 1984; Vaganov et al. 1985). The greater cell wall thickness compared with tracheids differentiated at the beginning of the growing season is one of the main criteria of definition of latewood. Until now the issue is not solved as to how the transition from formation of earlywood to formation of latewood is regulated. In any case such a transition is connected with the control of synthesis of the secondary wall. External and internal factors can influence formation of the secondary wall. Experimental research shows that seasonal change of external factors, such as light exposure, photoperiod, water deficit, nutrients, or temperature influence both the quantity of latewood cells and the thickness of their cell walls (see Larson 1969; Creber and Chaloner 1984; Zahner 1968; Savidge 1996; Wilson 1964; Brown and Sax 1962; Antonova and Stasova 1993; Vaganov et al. 1985; Denne and Dodd 1981; Carlquist 1988a,b; Downes and Turvey 1990; Lev-Yadun and Aloni 1995).

In early works conducted by Wodzicki (1971), Skene (1972) and Denne (1971a) it was pointed out that the rate of cell wall deposition varied relatively little within a growing season. For example, in spite of differences in the growth rates of individual trees (different tree vigor), the actual rate of deposition of cell wall material was about 0.1-0.2 μm^2 per day and seemed to show little change during the course of the season in *Tsuga canadensis* (Skene 1972). The time period required for lysis of the cytoplasm was about 4 days, with no evidence of any changes with tree vigor (Skene 1972). For tree rings of Douglas-fir (*Pseudotsuga menziesii*) it was 4-5 μm^2/day, and in trees with a well-developed crown at the beginning of a season 6-7 μm^2/day (Dodd and Fox 1990). These authors have compared rates of radial growth and formation of the cell wall in young trees distinguished by development of the crown, and for different heights in the stem. The differences are not marked, except in the case of the growth rate in the second half of a season in trees with a well developed crown. The experimental data of Wodzicki (1971) have shown that the rate of maturation has no clear influence on the radial size and thickness of the cell wall, and the main role is played by the duration of these stages of differentiation. The average value of the rate of cell wall deposition in *Pinus sylvestris* was a little more than in *Tsuga* and *Pseudotsuga,* reaching 5-10 μm^2/day. Similarly, Sviderskaya (1999) obtained a rate of cell wall deposition of 5-7 μm^2/day in observations of seasonal tree-ring formation in three coniferous species (*Pinus sylvestris, Picea obovata, Abies sibirica*). So, as in the case of the radial cell dimension of the tracheid, the experimental data on the kinetics of cell wall deposition indicate that the average rate of deposition of cell wall does not differ much during the growing season and supports the statement that the leading role in determining final cell wall thickness is

played by the duration of this process and by the radial size of the tracheid in which the cell wall was deposited.

Mechanisms for the control of tracheid radial expansion, and hence, through the predetermination of final tracheid radial dimension, cell-wall thickness, may be mediated through control of the rates of synthesis of different components of tangential and radial walls. The average rate of deposition of the cell wall does not differ much during the growing season and supports the statement that the leading role in determining final cell wall thickness is played by the duration of this process and by the radial size of the tracheid in which the cell wall was deposited.

The process of tracheid differentiation is, as a matter of fact, a process of implementation of the genetic program of differentiation, starting at the level of cambial cells and finishing with secondary cell wall formation (Graham 1996; Fukuda 1996; Hertzberg et al. 2001; Chaffey et al. 2002; Ito and Fukuda 2002; Kirst et al. 2003; Goujon et al. 2003; Nieminen et al. 2004). Schrader et al. (2003), for example, showed that the expression of specific members of the auxin transport genes are associated with different stages of vascular cambium development and demonstrate that trees have developed mechanisms to modulate auxin transport in meristem in response to developmental and environmental cues. A variety of anatomical parameters of tracheids among trees and years indicate that the eventual result is not absolutely determined, and that it depends on the local conditions where the differentiation occurs. The process of differentiation can be presented as a series of events, in which the duration and intensity of each stage depends on the previous one. Then, in changed conditions, if two events are carried on further in space and in time, their deterministic relationship may change. If we identify processes most sensitive to the influence of external factors, we see that the external signal should be most clearly perceived by the cambial zone. These external effects will leave their mark on further processes of differentiation and, ultimately, the anatomical characteristics of tracheids. As a result, the direct influence of environmental conditions on the process of tracheid enlargement, as recorded in their final anatomical characteristics, will be significantly smaller. There are a number of indirect data that indicate that the events occurring during cell division in the cambial zone can have a strong influence on the ultimate sizes of tracheids. Already, at this early stage of differentiation, biochemical changes of the primary cell wall are necessary for radial growth of cells and determination of its rate (Catesson 1990, 1994; Taiz 1984; Pritchard 1994).

In a recent review, Somerville et al. (2004) stated that progress integrating biophysical, developmental, and genetic information into useful models of plant cell wall will require a system-based approach. They presented a cyclical diagram which emphasizes that the expansion of the cell wall and integration of a new cell plate during cytokinesis are components of the cell cycle. "Thus, we infer that many of the genes involved in primary cell wall synthesis and modification will be found to be controlled by factors that control other aspects of the cell cycle" (Somerville et al. 2004, p.2210). This determines the bridge between first and last stages of tracheid differentiation through the activity of genes involved in the cell cycle and cell wall thickening.

Toward a quantitative description of cambial activity and xylem differentiation under environmental control.

Thus, to correctly describe the transformation of climatic signal to tree ring growth and wood structure it is necessary (according to the hormonal theory) to describe the mechanism of substrate and hormonal regulation of cambial growth and differentiation. This hypothesis of "independent" external control of wood formation offered by Larson (1964) is the main barrier to the creation of process-based models for dendroclimatology.

The hypothesis of "independent control" can be illustrated by the following. In a period of active wood formation, cells are in all three main stages (but at different locations within the forming tree ring), i.e. the external signal may affect cells in all stages at the same time. According to this we may write that

$$\frac{d\mathrm{N}}{d\mathrm{t}} = f_1\{\mathrm{x}_i(\mathrm{t}_j)\}$$

$$\frac{d\mathrm{D}}{d\mathrm{t}} = f_2\{\mathrm{x}_i(\mathrm{t}_j)\} \tag{1}$$

$$\frac{d\mathrm{CWT}}{d\mathrm{t}} = f_3\{\mathrm{x}_i(\mathrm{t}_j)\}$$

Where *i* indicates the factors or processes affected, and all three functions are assumed to be different and have a different time-dependence. Then in the final tree ring, each of its subdivisions (portions) will contain the climatic signal, integrated in time, accumulated in cell number (N), cell dimension (D), and cell wall thickness (CWT).

$$TR_{\mathrm{portion}} = f\{f_1[\mathrm{x}_i(\mathrm{t}_j)], f_2[\mathrm{x}_i(\mathrm{t}_{j+k})], f_3[\mathrm{x}_i(\mathrm{t}_{j+m})]\} \tag{2}$$

Here, j, k, and m are the time intervals between the processes of production, cell enlargement and wall thickening. The values of j, k, and m vary significantly during a season, and show a significant relation with the total number of cells in the cambial zone and total production (tree ring width). Taking into account that the process of enlargement of a single cell can continue up to 3 weeks, and that wall thickening takes 2-3 weeks, leads to the conclusion that each portion of a tree ring integrates the growth conditions over about 1.5 months (without any delays in passing the hormonal signal from apical meristem to cambium). The most complex aspect of this is the necessity of defining each function in the equations (1), which are assumed to be different.

According to this statement, the maximum density of the last forming portion of a tree ring must be determined only by the climatic conditions at the end of the growing season because all processes involved occur at this particular time. This means that even in strong temperature-limited conditions, the maximum density must be related strongly to August-September temperature, when the last forming tracheids enlarged and thickened. But almost all results in dendroclimatic interpretation of maximum density show that maximum density is better than even the tree-ring width as an indicator of the whole summer temperature because of significant correlation with the early season as well as with late season temperatures (commonly with April-September temperature) (Briffa et al. 2001, 2004).

An alternative hypothesis is that the main target of environmental control in tree ring seasonal formation is the cambial zone, and then this signal is transformed into further processes of cell differentiation (enlargement and cell wall thickening). This hypothesis suggests that the main target of environmental control is the first process; i.e. the cambial zone plays the main role as the target of environmental influence and then transforms this influence to the next stages of cell differentiation (Vaganov et al. 1985; Vaganov 1996):

$$\frac{d\text{N}}{d\text{t}} = f_1\{\text{x}_i(\text{t}_j)\}$$
$$\frac{d\text{D}}{d\text{t}} = f_2\{f_1\}$$
$$\frac{d\text{CWT}}{d\text{t}} = f_3\{f_1, f_2\} \tag{3}$$

There are several theoretical and experimental prerequisites:
1. The hierarchy of control simplifies the common mechanism of environmental control.

2. There is much evidence of a close relationship between the rate of cell production and the anatomical characteristics of the cells produced, i.e. the relationship between two consecutive stages of cell differentiation.

3. The cell dimensions (radial diameter and cell wall thickness) are mainly determined by the duration of these processes rather than their speed.

4. There is evidence of a non-random relationship between the radial dimension and cell wall thickness (i.e. a relationship between the second and third main processes of cell differentiation).

5. From measurements of interannual variability of tree ring characteristics there is a decrease in variability from a maximum for tree ring index (width), to a minimum for radial cell dimension (diameter, cell wall thickness, maximum density). This suggests a decreasing influence of climatic variations if one considers the within-ring components, in contrast to interannual ring with variability.

In the case of hierarchy control, the quantitative description becomes simpler because only one function must be defined in relation to environmental variables, and to do this we have enough experimental data from biophysical and physiological research of tree growth. This background allows us to create a simple version of the process-based model of tree ring formation under changing climatic conditions (weather conditions), and test this model by simulation of climatically-induced variations of tree ring width and cell dimension in different climates (from northern timberline to semi-arid region) (Vaganov et al. 1990; Fritts et al. 1991; Shashkin and Vaganov 1993, Evans et al. 2006, Vaganov et al. 2006). The basic premise of the model is the principle of a limiting factor, well known in the physiology of plant growth. The model is restricted by application only to the quantitative description of climatically-induced growth variations, which means that we do not use this approach for other factors controlling tree growth like fertilization (either carbon dioxide or nitrogen), within stand competition, growth release after forestry management, etc.

A significant property of this model is its use of available, commonly measured meteorological characteristics available from any meteorological station. The model, therefore, consolidates and compresses our recent knowledge concerning the climatic influence on tree growth, and on the other hand, improves our understanding of the tree growth-climate relationship. There are several examples and issues that illustrate the advance in tree growth-climate relationships resulting from the use of the model as a research tool.

Process Model Description

The Vaganov-Shashkin (VS) model makes use of a limited number of equations relating daily temperature, precipitation, and sunlight to the kinetics of secondary xylem development (Vaganov et al. 2006) in order to model tree-ring growth and the internal characteristics (density, cell sizes) of annual rings. The model consists of two primary modules, or blocks. The Growth (or Environmental) Block calculates a daily external growth rate based on climatic variability, including temperature, soil moisture balance and solar irradiance. The Cambial Block uses this external growth rate to simulate the rate and timing of growth and division of cells in the cambium following the hierarchical model described above. In this way, the kinetics of xylem formation are explicitly modeled as a function of climate variability modified by parameterized environmental and cambial processes.

Growth (Environmental) Block

Relative growth rate calculations made by the model are used to determine the rate of the growth and division of cells during xylogenesis, as well as the timing of the transition between stages. Daily growth rates themselves are determined by comparing daily temperature and soil moisture (calculated from precipitation, transpiration, and soil drainage) to piecewise linear approximations of parabolic growth functions (**Figure 3, inset**). Four parameters define the shape of the trapezoidal growth functions – a minimum ($g(t) = 0$), a lower and upper optimal bounds ($g(t) = 1$), and a maximum ($g(t) = 0$). Between minimum (or maximum) and the lower (or upper) bounds of the optimal values for the climate parameter (temperature, sunlight, or soil moisture), growth rates will be between 0 and 1. Relative growth rates are calculated for precipitation ($g_W(t)$), temperature ($g_T(t)$), and sunlight ($g_E(t)$). The determination of the overall growth rate $G(t)$ for any given day t is calculated as

$$G(t) = g_E(t) \cdot \min\left[g_T(t), g_W(t)\right] \tag{4}$$

Water balance is computed daily by the model as a function of precipitation (as well as snow melt), evaporation (which is function of temperature), and runoff (Thornthwaite and Mather 1955). Solar irradiance is determined by the model from the latitude of the meteorological station from which the input data is taken. Because of the minimization term in the calculation of the growth rate, and the piecewise approximation of the nonlinear growth function, the model behaves stoichiometrically, controlled by the most limiting factor (e.g. Fritts 1976), at a daily resolution.

Cambial Block

The Cambial Block uses the output from the Growth Block to determine the rate at which cambial cells grow and divide (**Figures 2, 3**). Each cell in the cambial block is characterized by two variables at each daily step – its position (j) in the cellular file and its diameter. The growth rate $G(t)$ calculated in the prior block is used to derive a specific growth rate, $V(j,t)$, for each cell based on its position (**Figure 2**). For cambial cells, diameter increases in the G_1 phase until a maximum size when division occurs, or until the cell loses the ability to divide as its growth rate falls below a minimum threshold $V_{min}(j)$ for the cell's position in the radial file. Cells which lose the ability to divide pass out of the cambium, and complete the cell cycle, including elongation and cell wall thickening. Daily cellular growth rates below a critical minimum threshold (V_{cr}) send the cambium into dormancy. The cells in the cambium at the end of one simulated growing season will therefore be those which first grow and divide in the subsequent year, and therefore influence the cambial dynamics and tree-ring structure of the following year. Activity in the cambium is initiated each year when the sum of temperatures above a certain threshold over a specified period of time (i.e. growing degree days) reaches a critical threshold.

It should be noted that, so operationalized, the Vaganov-Shashkin model captures and explicitly integrates the essential features of cambial dynamics as previously described. Annual xylem cell production is related to the number of cells in the cambial zone, the size of which varies over the course of the year in response to environmental variability. Specific cellular growth rates are positional and depend on the distance of the simulated cell from the cambial initial, with maximum rates of cell division observed tangential to the zone of radial expansion (the `cambial edge'). Radial tracheid dimension is mainly determined during cell production and at the beginning of expansion.

The model uses daily precipitation and temperature from meteorological stations as its required input data. The 28 primary model parameters are based on empirical and experimental data, whose selection is discussed in detail by Vaganov et al. (2006). The output, consisting of standardized synthetic tree-ring width chronologies, simulated growth rates, and number of cambial cells, are solely a function of those environmental and biological activities modeled in the Growth and Cambial Blocks. Hence, simulations do not reflect direct growth influences due to increasing atmospheric carbon dioxide concentration over the past 150 years. Nor are additional biological or ecological influences on patterns of tree ring formation modeled, including those due caused by tree age or geometry, interseasonal carbon storage, canopy and

root activity, or stand-level competition and disturbance. In a sense the simulations can be considered 'idealized' mean site tree-ring chronologies with respect to the modeled processes.

Model Applications

Temporal variability in the relationship between climate and tree-ring derived proxies have been identified in a range of species and locations (Briffa et al. 1998a,b; Biondi 2000; Jacoby et al. 2000; Aykroyd et al. 2001; Wilmking et al. 2004, 2005). Such instability might be particularly important in environments where both temperature and precipitation can be important controls on tree growth (Anchukaitis et al. 2006), where the timing of the onset of growth or the length of the growing season strongly influences tree-ring proxies (Vaganov et al. 1999; Aykroyd et al. 2001; Vaganov et al. 2006; Evans et al. 2006), and for high latitude or high elevation temperature-sensitive trees under anthropogenic climate forcing (Jacoby et al. 2000; Wilmking et al. 2004, 2005). The Vaganov-Shashkin model produces synthetic chronologies that would be expected if climate, mediated by cambial processes, were the only external control on tree growth. This potentially allows dendroecologists to evaluate the importance of hypothesized ecological factors that might be responsible for differences observed between actual tree-ring chronologies and simulations. For instance, it can also be used to develop null hypotheses against which to test theories about the influences of insects, disease, CO_2 enrichment, carbon storage, pollution, and disturbance on tree growth. Furthermore, because the Vaganov-Shashkin model has the ability to simulate nonlinear relationships between tree-ring formation and the environment, it can be used to determine whether observed variability in climate-tree growth relationships arise as a function of climate itself, as a stochastic feature without a determinant cause, or through possibly unobserved influences by biological or ecological changes not related to climate.

The Vaganov-Shashkin model has recently been applied to simulate tree-ring proxies across a range of environments for a variety of species and using several complementary approaches. The particular methodology for developing and analyzing synthetic chronologies depends in part on the research questions posed and the availability of meteorological and tree-ring data with which to drive and evaluate the model. The simplest approach to modeling tree-ring chronologies is to use single meteorological stations close to the actual tree-ring chronology site. Several studies have demonstrated that using appropriately chosen local meteorological stations can produce simulations which skillfully reproduce actual tree-ring width patterns (Vaganov et al. 1999, Evans et al. 2006, Vaganov et al. 2006). These studies target cases in which direct model-data

intercomparisons are easily made, but do not assess the extent to which model skill is general across environments and species. An intermediate approach exploits spatiotemporal techniques like principal components analysis (PCA), which decompose a large set of time series into a few low-order empirical functions that contain the primary modes of robust common variance in networks of observed and simulated tree-ring data networks (Anchukaitis et al. 2006). A third approach is to compare tree-ring datasets to meteorological datasets on a large scale for assessing model robustness and the general suitability of the tree-ring dataset for climate monitoring (Evans et al. 2006). These nonlocal approaches permit assessment of the suitability of the proxy data network for the reconstruction of large-scale features of paleoclimatic fields, but the comparison suffers from differences in the meteorological and dendrochronological observing networks (Evans et al. 2006, Anchukaitis et al. 2006) which make direct comparisons impossible.

Local simulations.

Evans et al (2006) reported tree-ring width simulations performed for eight high latitude Russian sites (Vaganov et al. 2006) spanning 60 degrees of latitude (**Figure 4**), all using the same set of fixed parameters. Despite neglecting adjustment of model parameters to fit local site characteristics, 7 of 8 simulations are significant at or above the 95% confidence level. 4 of 8 correlations between 5-year means of the simulations and actual chronologies were significant at or above the 90% confidence level. Analysis of more extensive results (Evans et al. 2006) showed that decadal-scale variations in actual tree-ring data were skillfully modeled in about 25% of cases. A similar result was found using classical statistical modeling techniques, suggesting that care must be taken when interpreting decadal-timescale features in tree-ring data as climatically-driven.

Cook and Pederson (2006, this volume) discuss the problem of emergent phenomena in dendrochronology and the resulting uncertainties in statistically modeling tree-ring data, using as a case study tree-ring chronologies of a number of species and locations from near the Mohonk Lake, NY meteorological station. Their work raises the question: How do we separate empirically-demonstrated emergence, pervasive in the biological sciences from incomplete understanding of the system at hand? In an effort to address this question, we simulated the NY004r.crn Mohonk Lake tree-ring width residual chronology (http://www.ncdc.noaa.gov/paleo/) using the Vaganov-Shashkin model and Mohonk Lake station daily meteorological data (NCDC Cooperative Station 305426).

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We found that with only an increase in the soil moisture drainage rate (all other model parameters at default 'Russian' settings; Anchukaitis et al., 2006, Vaganov et al., 2006), the simulation was sufficient to explain the gross features of this data series (annual r up to 0.57 ($p<0.05$; **Figure 5c**). The significance of r was not highly sensitive to the exact value of soil moisture drainage parameter we chose. Correlation functions for simulated and actual chronologies are similar (**Figure 5a, 5b**). The most important of these are (1) positive correlation with current-year May-July precipitation, (2) negative correlation with current-year May temperature; (3) positive correlation with current-year March/April temperature; (4) positive correlation with prior-year September/October precipitation. Lower frequency model skill may be a consequence of the influence of the size of initial cambial cells from the prior growing season on the ring width of the following year (results not shown).

Although Cook and Pederson (2006, this volume) pointed to observation (3) above as an example of an emergent phenomenon, it is predicted with the VS model simulation. Examination of the growth-limiting functions G_T, G_E, G_W and the integrated growth function G broadly confirm these results for an average year based on 1925-1973 simulations (**Figure 5d**). The modeling results suggest that early season growth is strongly tied to the timing of early spring (March) warming, unless such warming is strong enough by early summer (May), in which case warm conditions lead to growth limitation by moisture stress. The way in which the VS model simulates such a phenomenon is described in Evans et al. (2006). Given these results, maybe in this specific case it's not emergence after all. Our tentative conclusion is that current-generation multivariate linear regression models may be unable to completely describe the environmental controls on tree-ring variations because of intraseasonal-interannual changes in the limiting factors controlling tree growth (see also the example from Anchukaitis et al. (2006), described below). Forward modeling exercises like this can complement statistical model verification procedures, assess the influence of such effects in linear paleoclimate inversions, increase confidence in our interpretation of the data ("What do we expect to see?"), and help further distinguish emergence from statistics.

Mesoscale network simulations.

Anchukaitis et al. (2006) used the modified parameter described for the Mohonk simulations above to simulate tree-ring widths across the southeastern United States. They demonstrated that the leading principal component time series of simulated and real conifer chronologies is well-

correlated and that both reflect the regional importance of spring rainfall for interannual variability in tree-ring widths (**Figure 6**).   Anchukaitis et al. (2006) further apply the model to detecting and attributing changes in climate/tree-ring growth relationships related to climate. Using the eight simulations from the southeastern United States validated against the leading temporal pattern of variability in actual tree-ring chronologies, they hypothesize that tree-ring growth should become increasingly limited by summer precipitation. Model findings are verified using a new tree-ring chronology, excluded from the original dataset, which shows a similar pattern of increased growth sensitivity to summer precipitation, and is consistent with analysis of trends in regional climate and broad-scale forcing (Anchukaitis et al. 2006). Additional tree-ring data, updated through the most recent quarter century, should show the same behavior, if the model-based hypothesis is correct. The results point to larger scale predictive studies using the VS model driven by general circulation model (GCM) output.

Large network intercomparisons

Evans et al. (2006) used a continental-scale set of meteorological stations and tree-ring chronologies to assess the skill of the Vaganov-Shashkin model across a broad range of species and environments. They utilized a 500km search radius around each of 190 tree-ring chronologies to evaluate simulated chronologies derived from the Global Historical Climatology Network (Peterson and Vose, 1997) within that area. This approach allowed the model to choose the station within the given search radius which resulted in the best simulation, and presumably best reflecting climate conditions at the actual tree-ring chronology site. This approach assumes that a single station exists within the search radius that best approximates the mean conditions over a given region. A similar search radius approach has been successfully used in point-to-point regression-based reconstructions of the Palmer Drought Severity Index using tree-rings Cook et al. (1999, 2004). Evans et al. (2006) found that the model simulated chronologies were correlated at the 95% significance level with actual tree-ring chronologies in 176 out of 190 cases (**Figure 7**). The results were not dependent on the size of the search radius, with similar findings for a 200 km search area (Evans et al. 2006, results not shown). Process model skill was about the same as that achieved for verification-period statistical modeling of the same chronologies using robust linear multiple regression methods common in dendroclimatology. Skillful decadal simulations were only made in a minority of simulations either by statistical modeling or process modeling approaches, suggesting that paleoclimatic interpretations of decadal climate variability from tree ring width data should be made with caution. Additional

studies designed to identify and remove non-climatic biases from candidate proxy paleoclimatic datasets are underway.

Conclusion

By linking the external environmental controls on the formation of tree-ring proxies to processes which primarily influence the cambial zone, the VS model allows us to produce synthetic tree ring series which can be compared directly to actual tree-ring based proxy observation of climate variability. In cases where robust coherence between model results and actual data is found, we can use the model to mechanistically interpret the basis of variations in the actual tree-ring data. Local, regional and synoptic-scale intercomparisons of model results and data suggest the VS model explains gross features of interannual tree-ring width variability which are relatively insensitive to parameter estimation. These results can be used to better understand the processes underlying behavior of the actual data. In the case studies discussed here, for instance, the apparent emergence of behavior such as the dependence of eastern Hemlock ring-width variations on spring temperatures, and the increasing dependence of ring width variations in the southeastern US on summertime soil moisture, can be explained in terms of intra-annual to multidecadal changes in environmental conditions, as mediated by cambial processes. Future applications of the model may include further exploration of the biological basis of emergent phenomena, study of the nature of decadal-scale variability in tree-ring data, prediction of the influence of future climate change on conifer forest growth, objective process-based removal of potential nonclimatic biases in tree-ring data prior to paleoclimatic inversions, and the allowance for varying climate-tree growth relationships as a constraint in paleoclimatic modeling and reconstruction activities using tree-ring data as input.

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Figure captions

Figure 1. Seasonal dynamics of (1) radial tracheid size, (2) cell number in cambial zone, and (3) specific growth rate in (a) *Abies sibirica* and (b) *Pinus sylvestris* (Sviderskaya 1999). A good relationship is seen between the intraseasonal changes in the specific growth rate and changes in the size of tracheids leaving the cambium. The radial tracheid dimension is primarily determined by the average radial growth rate in the cambial zone or by the average rate of cell division within the cambial zone, and therefore also corresponds quite well to the magnitude of cell production.

Figure 2. Schematic diagram showing the functions which control cell division and transitions in the Vaganov-Shashkin model. The rate of cambial cell division (which is proportional to the cellular growth rate $V(j,t)$) is a linear function of the position (j) of the cell in the cellular file and the daily external environmental growth rate $G(t)$. The division rate increases with distance from the cambial initial. The exponential function $V_{min}(j)$ defines the threshold rate of division, below which cells lose the ability to divide and mature to xylem cells. The size of the actively dividing cambial zone is therefore a nonlinear function of the rate of cellular division. The third function, V_{cr}, defines the division rate at which cells still in the cambium enter dormancy.

Figure 3. Vaganov-Shashkin growth and cambial model block processes. Daily external (environmental) growth rates are determined by comparing daily temperature and soil moisture (calculated from precipitation, transpiration, and soil drainage) to piecewise linear approximations of parabolic growth functions (*see inset*) in the Growth (Environmental) Block. This growth rate is used in the Cambial Block to calculate the cellular growth rate $V(j,t)$, which is a function of the environmental growth rate and the position of the cell in the radial file. Each cell is permitted to be dormant, differentiate, grow, or divide on an intraday time interval. When a non-differentiated cell reaches a critical size, it enters and completes the mitotic cycle, continuing its subsequent grow at a constant, environmentally-independent growth rate until division occurs, resulting in two cells each half the size of the original mother cell.

Figure 4. Time series of Vaganov-Shashkin model simulations from high latitude sites across Russia. Correlations are for annual and five year averages. *, **, *** indicate one-tailed significance at $p<0.1$, 0.05, 0.01 levels, respectively, considering effective degrees of freedom given series lag-1 autocorrelations. (a) Coku (147.9E, 70.6N). (b) Hatanga (102.5E, 72N). (c) Olenek (112.4E,68.5N). (d) Tura (100.0E, 64.2N). (e) Turuchan (88.0E, 65.8N). (f) Ulan-Ude (107.4E, 51.8N). (g) Verhoyn (133.4E, 67.6N). (h) Zigansk (123.4E, 66.8N). Results from Evans et al. (2006).

Figure 5. Simulation of Mohonk Lake tree-ring width chronology. Correlation of previous and current year tree-ring widths with (a) temperature and (b) precipitation show similar patterns for both simulated and actual chronologies. Dashed lines of the same color show the 95% two-tailed confidence intervals from bootstrapping (1000 draws with replacement). (c) The simulation (black line) is correlated with the actual chronology (gray line) at $r = 0.57$ ($p < 0.05$). (d) Growth functions G_T, G_W, G_E and overall growth function G from daily simulation output averaged for 1925-1973. See text for discussion.

Figure 6. Intercomparison of synthetic and actual tree-ring width chronologies from the southeast United States. (a) Leading time series expansions from PCA on simulated and actual regional ring width data (black and gray lines, respectively). Correlation fields between the spring (MAM) precipitation and the first principal component for the (b) simulated and (c) real tree-ring width chronologies for the full period of overlap (1920–1985). Four-letter identifiers

mark eight meteorological stations in Figure 6b; three-letter identifiers denote 10 ring-width chronology sites in Figure 6c). Reprinted with permission from Anchukaitis et al. (2006).

Figure 7. Significance of annual correlations of simulated and actual tree-ring width data for 8 sites across Russia (Figure 4) and 190 sites in North America from the Mann et al. (1998) dataset. Black and grey circles show correlations with significances at or above the 99% and 95% levels, respectively; white circles show significances below the 90% level. Reprinted with permission from Evans et al. (2006).
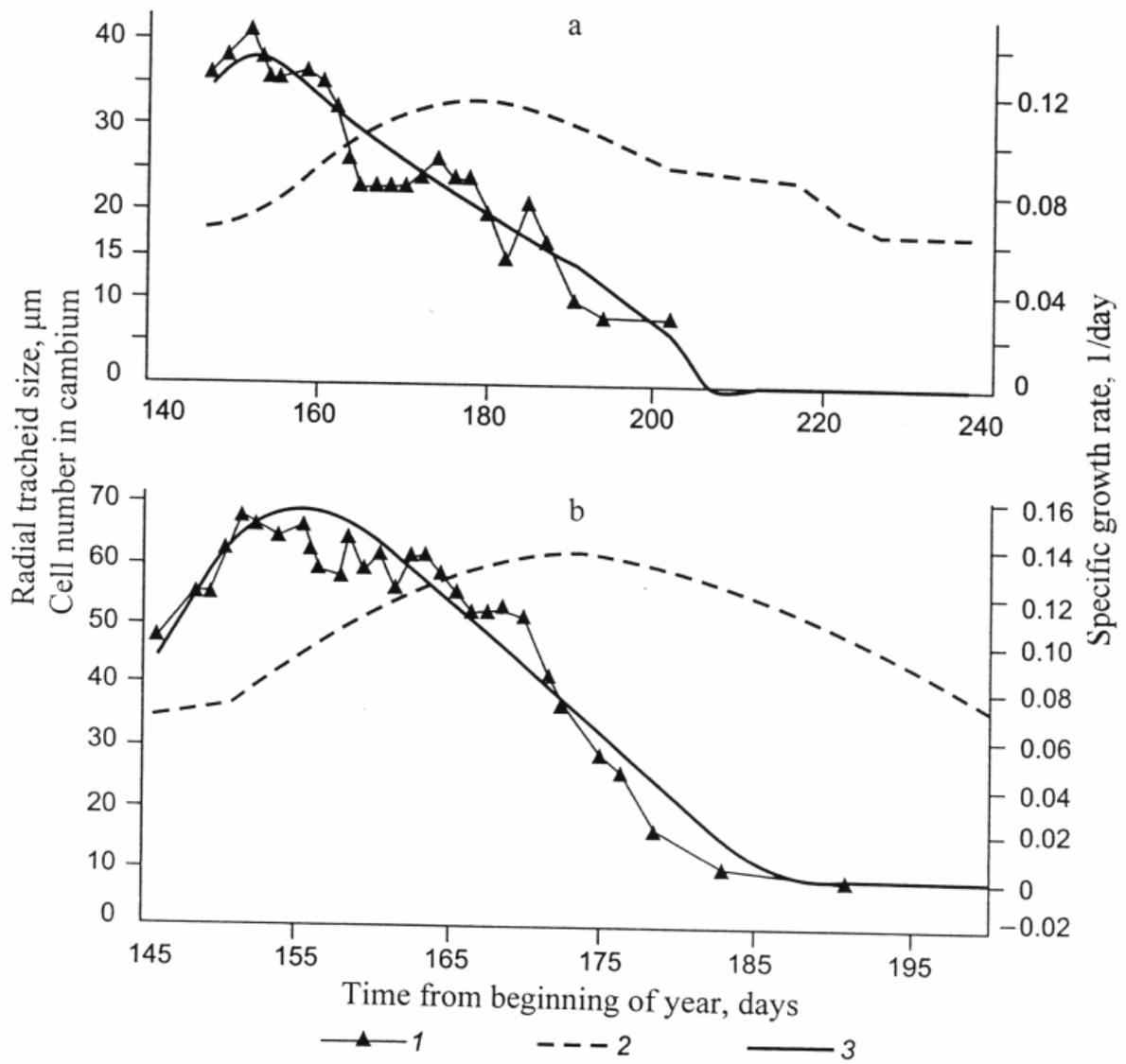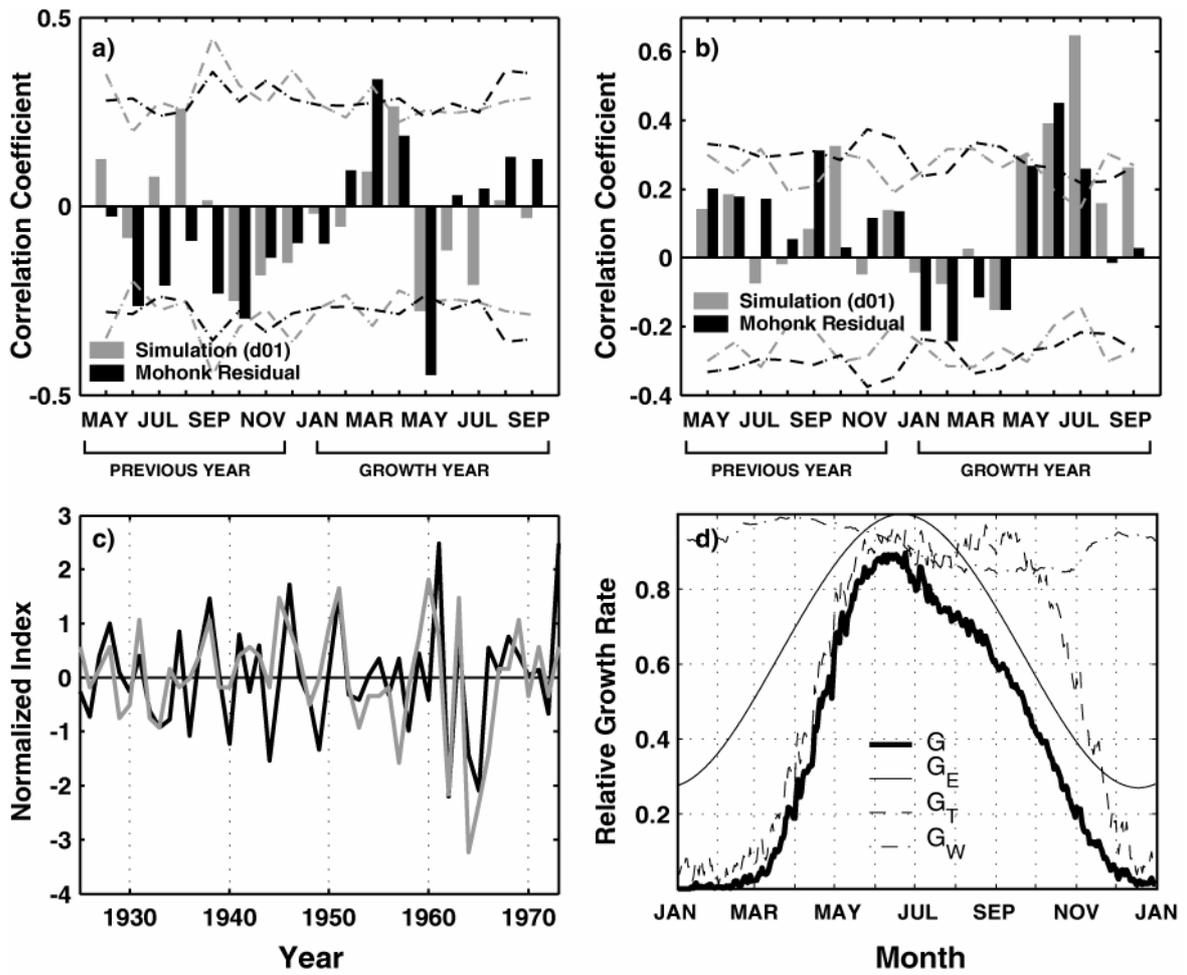
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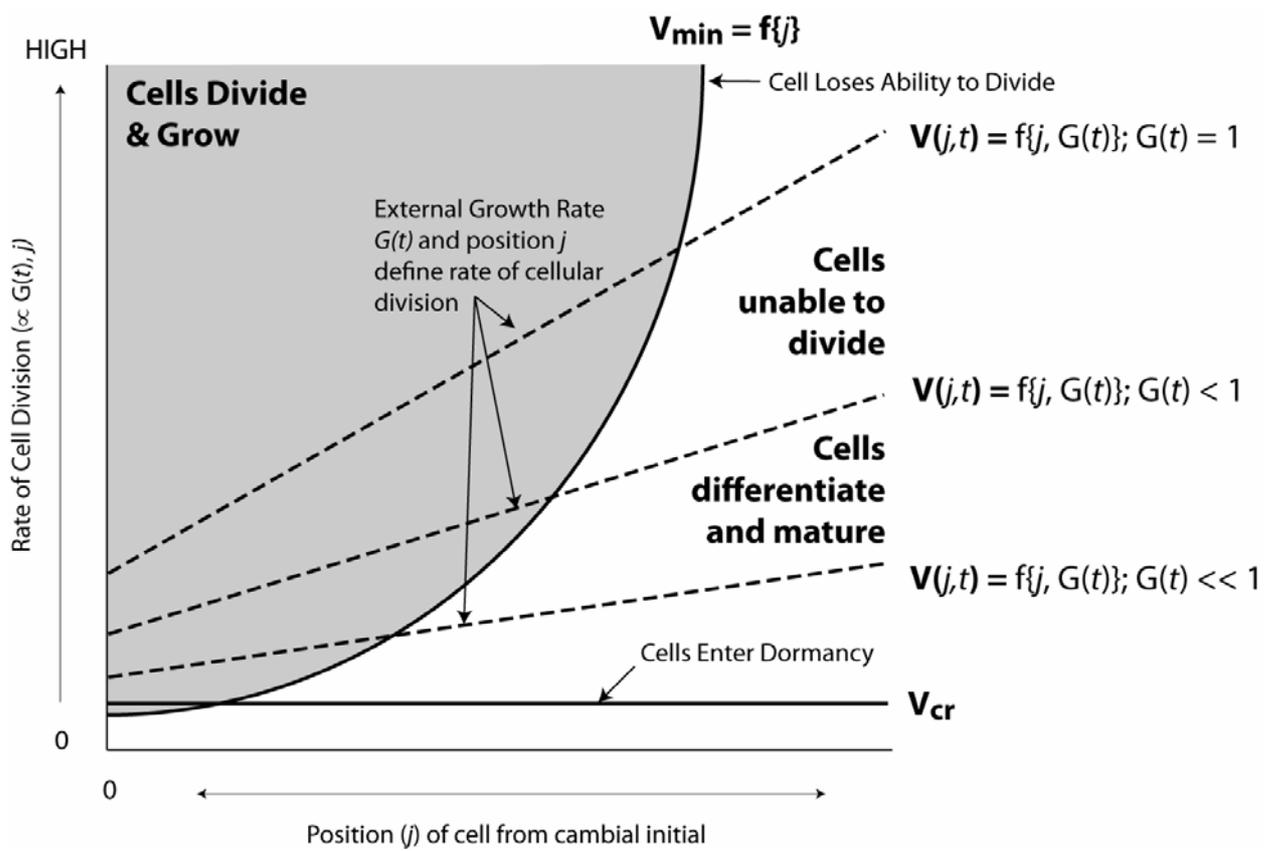
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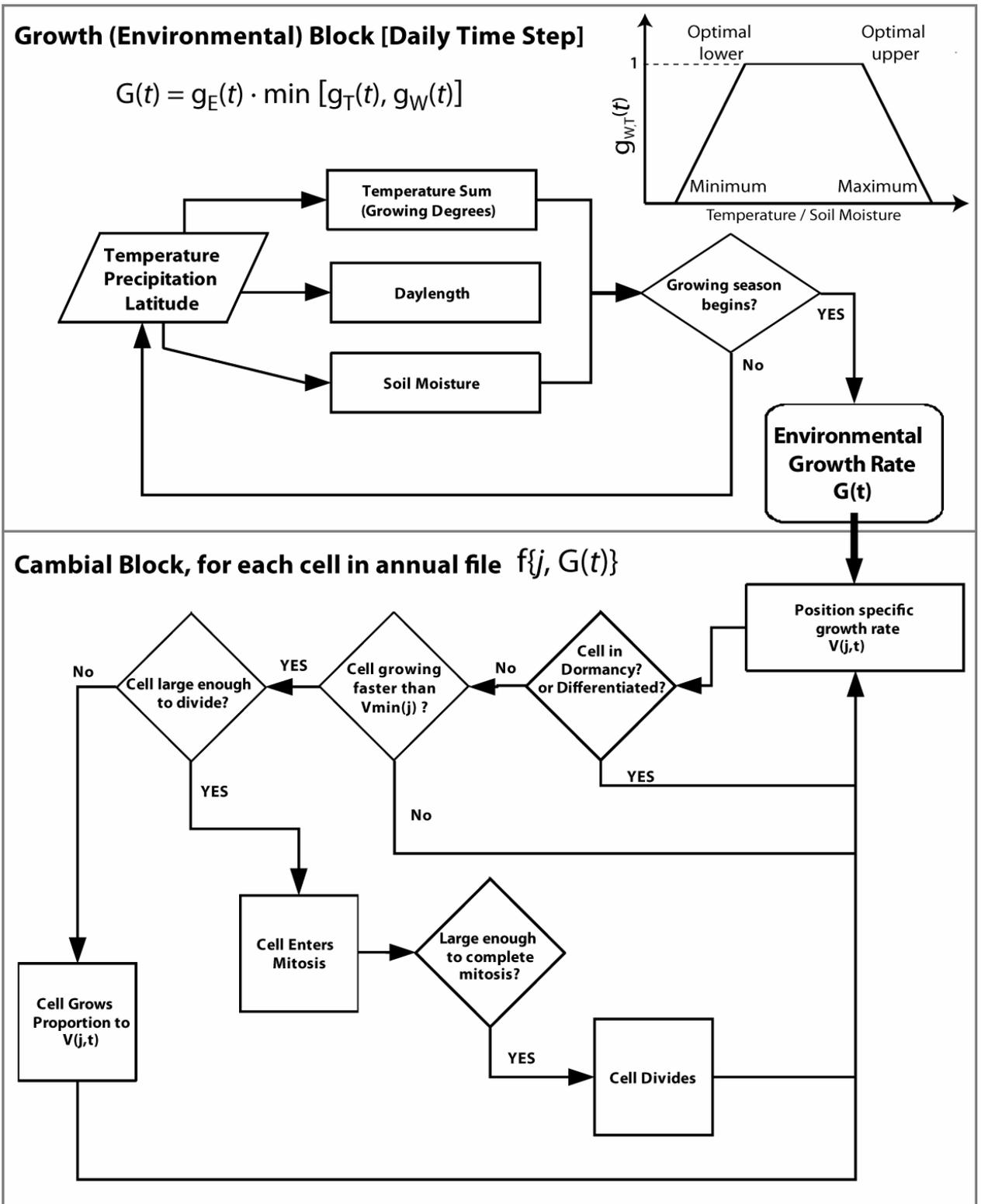
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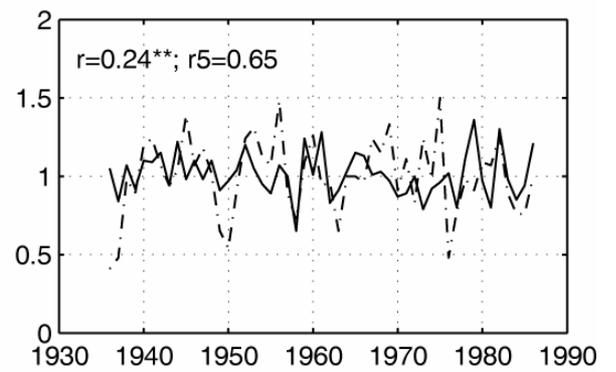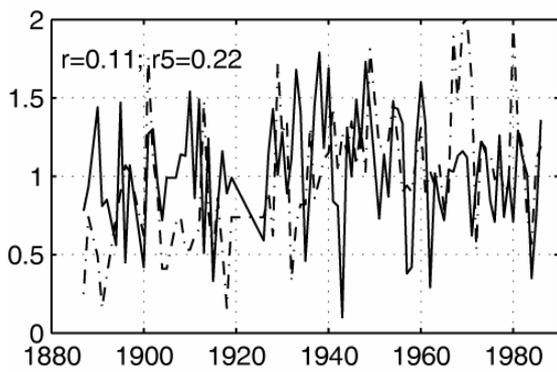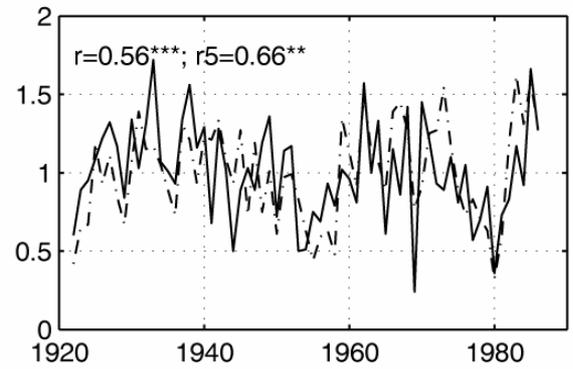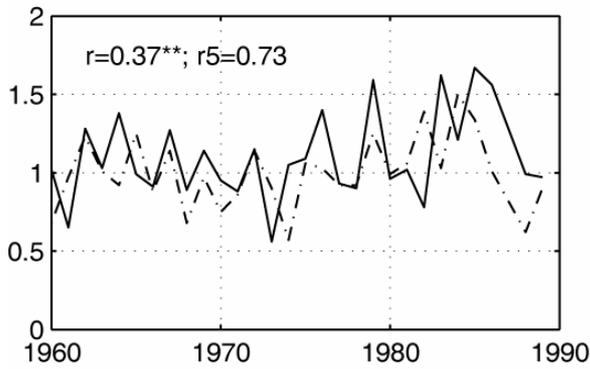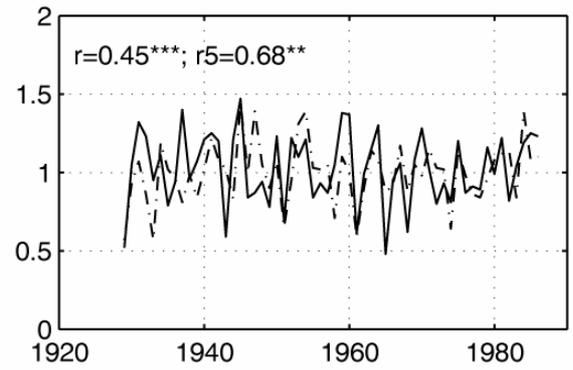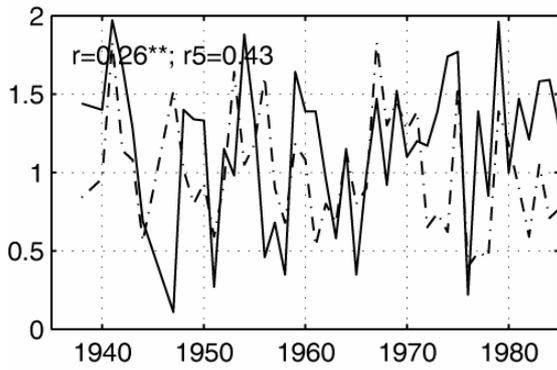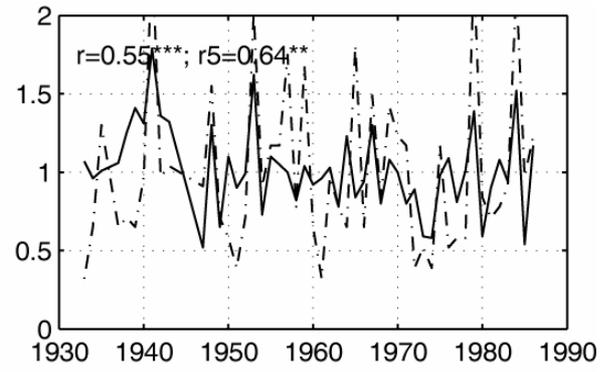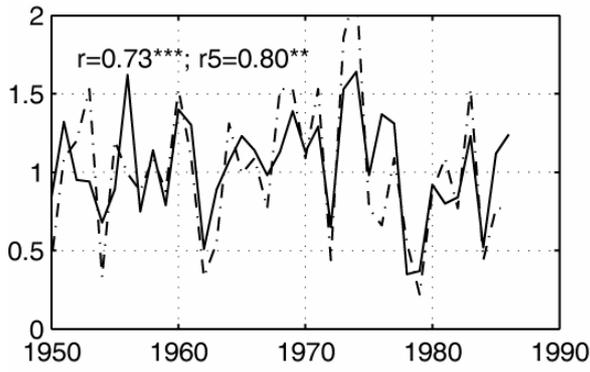
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