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## **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 an 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 phenomena and prediction of the influence of climate change on conifer tree growth dynamics.

### **3.1 Introduction**

Climatic variation is a major factor affecting tree-ring growth and wood formation. Accordingly, a significant amount of dendroclimatology research has been 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; Cook et al. 2002; Briffa et al. 2004; Pederson et al. 2004; Watson and Luckman 2004; Salzer and Kipfmüller 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 1996a). 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 Harold 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, 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 prior 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), Howard and Wilson (1972), and Wilson (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).

### **3.1.1 The substrate source-sink hypothesis**

In his pioneering work on the biological basis for dendroclimatology, Fritts (1976) included extensive descriptions of the role of both metabolic and cambial processes as mediators of the environmental control on annual tree growth and ring formation. Metabolic approaches often rely on a source-sink understanding of the influence of climate on tree-ring width, which assumes that the environment indirectly determines annual xylem increment as a function of the amount of carbon available for secondary growth. Because secondary basal growth is interpreted to be a low priority for the apportionment of the available whole plant resources (Savidge 2000a), wider rings would arise as a result of optimal climatic conditions for photosynthesis, while a narrow ring would signal a deficit of carbohydrates and environmental conditions that restrict photosynthetic capacity. Clearly, given that a large quantity of complex carbohydrates, in the form of cellulose, lignin, and hemicelluloses and other polysaccharides, form the bulk of tree biomass, the availability of a source of carbon is an obvious prerequisite for secondary growth. Consistent with a carbon source-limited understanding of secondary growth, it has been observed that plant resources allocated to reproduction can result in a reduction of overall basal growth (Wheelwright and Logan 2004). Defoliation can also induce basal growth suppression and narrow tree rings (Speer et al. 2001), presumably through limitations on available carbohydrates (Ericsson et al. 1980).

Ecophysiological modeling of the environmental controls on the annual incremental basal growth has generally made use of this carbon-balance, source-sink

approach (Bassow et al. 1990; Makela 1990). In essence, this type of model focuses on how the external environment controls carbon fixation and the production of other metabolites by trees in the canopy (buds and leaves) and how these are then allocated to various plant parts. Carbon-balance models may include calculations of photosynthesis as a function of tree age, foliage and crown composition, height, and root mass (Bassow et al. 1990). Assimilated carbon is then partitioned into branch, bole, root, and crown growth, as well as to respiration. Explicit models linking environmental conditions to resultant 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 (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 have been a critical component of the science of dendrochronology. It is important to note here that Fritts' model, TREERING, is not purely ecophysiological. It uses photosynthesis and assimilation to modify the rates of cellular processes in the cambium (see next section), and is therefore a hybrid carbon-balance and cellular process model (Fritts et al. 1999). The MAIDEN model (Misson 2004) uses a stand-level ecophysiological approach, which simulates the environmental control on photosynthesis and respiration, using both climate and allometric data to determine carbon fixation and mean bole increment diameter, which can be interpreted as analogous to tree-ring width for comparison with dendroecological data.

A drawback to this approach is that modeling the partitioning of carbon within a tree depends strongly on parameters that are not completely understood or described (see LeRoux et al. 2001 for a review and critique). Further, there is evidence of age-related trends in partitioning coefficients (Makela 1990). Many allocation processes will scale with tree height, a non-climatic, age-dependent metric that is itself at least partially a function of stand-level competition for nutrients, sunlight, and water.

A further challenge to modeling the environmental control on tree growth is that our understanding of the nature of the relationship between the concentration of carbohydrates in the developing xylem and the eventual ring width as mediated by the external environment (climate, photoperiod, exogenous ecological factors) remains incomplete (Savidge 2000a, b). Earlier research found the amount of carbohydrates in the cambium was positively correlated with the period of greatest tracheid production (Parkerson and Whitmore 1972). However, Sundberg et al. (1993) revealed that the relative concentration of sucrose could not explain ring width differences between two populations of *Pinus sylvestris*. Similarly, a study of the effect of pruning *Eucalyptus grandis* trees revealed that the loss of stems and foliage does not reduce tree diameter (Thomas et al. 2006). Even extreme insect defoliation has been observed to not result in reduced-diameter growth or tree-ring width (Jones et al. 2004), even in one case despite a 50% reduction in the number of leaves, presumably because stored starches can compensate to some degree for the immediate loss of photosynthetic capacity (Hoogesteger and Karlsson 1992). Dickson et al. (2000) have hypothesized that the export of photosynthate could be generally sink limited as opposed to excess source mediated; that is, environmental constraints may reduce developing tissues' demand for metabolic products prior to the point in time at which photosynthesis or total

carbohydrate availability becomes truly limiting. Körner (1998) examined potential environmental controls on alpine tree-line position and found that trees in these environments were not limited by carbon availability and photosynthetic rate, but rather apparently directly by temperature. In a recent paper, Körner (2003) is even more direct:

It is concluded that, irrespective of the reason for its periodic cessation, growth does not seem to be limited by carbon supply. Instead, in all the cases examined, sink activity and its direct control by the environment or developmental constraints restricts biomass production of trees under current ambient CO<sub>2</sub> concentrations.

### **3.1.2 The cambial control hypothesis**

A different understanding of the environmental control on the characteristics of annual tree rings is that cellular processes in the cambium are directly influenced by environmental conditions. It is recognized that these cellular processes of growth, division, differentiation, maturation, and death, which do ultimately give rise to the structure and size of the annual tree ring, are controlled by gene expression and hormonal stimulus, and that they can respond to both external (environmental) and internal (developmental) influences (Savidge 2000a; Plomion et al. 2001; Schrader et al. 2003). Rossi et al. (2007) concluded that the minimum threshold temperature for growth they observed in tree-line larch, pine, and spruce was directly limiting secondary growth at the cellular level, and that below this temperature the sink for nonstructural carbohydrates in the secondary xylem was reduced. Numerous experiments have shown that direct heating of stems can initiate cambial activity after the onset of winter dormancy (cf. Gričar et al. 2006). Abe et al. (2003) found that cell expansion in the cambium decreases as a direct

consequence of water deficit, which results in an overall decrease in cell production as cambial activity subsequently declines. Cellular processes in the cambium can therefore be directly inhibited by climate, through temperature or pressure (via water potential) influences on the cell cycle. The impetus to avoid cavitation and cell embolism in vascular tissues would not require mediation through carbohydrate availability and could act as a developmental determinant on the cambium itself.

Hormones and other substrates clearly play an important role in cellular growth and differentiation in the cambium, although the exact mechanisms through which they influence these processes continue to be investigated (Savidge 1983, 1996, 2000a; Dengler 2001). Recent research on the genetic controls on xylem differentiation by Schrader et al. (2003) has shown that hormone gradients across the cambial zone are associated with differential gene expression and the specific stage of cellular development. Because of this, cambial processes and development of new xylem cells are inherently related to their position in the cellular file. Schrader et al. (2003) also concluded that the hormonal gradients across the cambium could change rapidly, potentially in response to external environmental influences. Similarly, Uggla et al. (2001) found concentration gradients of sucrose and indole-3-acetic acid (IAA) across developing vascular plant tissue that corresponded to different stages of cellular development, and moreover that the onset of latewood formation did not correspond to any seasonal change in overall carbohydrate availability. The importance of positional information and the rate of cellular processes, particularly division, in the developing xylem will be discussed below in the context of the physiological and observational basis for our model. Certainly, xylogenesis cannot occur without the provisioning of sucrose and hormones from the canopy, which in turn depends on access to water and nutrients

provided by the roots. However, cellular processes in the meristem and developing xylem directly regulate cambial activity, and secondary xylem development involves spatiotemporal gradients of cellular growth and regulation, which can reflect the direct influence of climate on these processes and patterns.

For dendroclimatology, it would be desirable to create a tractable forward model that mechanistically includes only the critical processes that are minimally necessary to 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, chapter 4, 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 (chapter 4, this volume) 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 that integrates the primary environmental controls on conifer cambial activity is described, and we provide examples of its application in dendroclimatology. A version of this model, here referred to as Vaganov-Shashkin (VS), also forms the core of 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.

### **3.2 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 their 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 (Wilson 1966; Schmid 1976; Catesson 1984; 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 (Wilson 1966; Gregory 1971; Skene 1972; Kutscha et al. 1975; Vaganov et al. 1985). In dormancy, the size of the cambial zone reaches a minimum and usually includes 4 to 5 cells but can reach up to

10 (Larson 1994). The radial diameter of cells in the cambial zone is equal to 5–6  $\mu\text{m}$  in average but does not exceed 10  $\mu\text{m}$  (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  $N_{\text{camb}} = 3.82 + 0.05 \cdot N$  ( $R^2 = 0.75$ ;  $n = 37$ ;  $p < 0.001$ ). Sviderskaya (1999) obtained similar results from seasonal observations of tree-ring formation in Scots pine (*Pinus sylvestris*) and Siberian fir (*Abies sibirica*) in the Siberian taiga (Fig. 3.1).

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 the 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 (Fig. 3.1). The average duration of the cell cycle in the cambial zone varies during a season. Usually the cycle is shorter when earlywood 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 one-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 the 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; Grillos and Smith 1959; Bannan 1962; 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 timberline 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 intraseasonal

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 the interannual deviation in total cell production and tree-ring width.

Analysis of the data shows that there are two determinants of variability in the sizes of the cambial zone: one that 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.

### 3.3 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, pp. 36–37). The visible result of the enlargement is greatly increased radial cell size. In earlywood the radial dimension of tracheids reaches 50–60  $\mu\text{m}$ ; in latewood it is about 15–25  $\mu\text{m}$ . So, during the formation of earlywood the radial size of tracheids increases up to 7 to 8 times, in latewood, up to 2 to 3 times in comparison with the starting size of a cell in a cambial zone, which is about 7–8  $\mu\text{m}$  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 (Fig. 3.1). 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 combine with the seasonal trend (a typical example of this is the formation of ‘false’ rings caused by intraseasonal drought) (Fritts 1976; Schweingruber 1988, 1996).
3. The average radial tracheid dimension is more or less constant over a long period of tree growth. This constancy 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  $\mu\text{m}$  (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 two to three 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 lasting only 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 nonspecific effects of hormones and other plant growth regulators (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 (Savidge 2000a; Baluska et al. 2001). 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<sub>1</sub>-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 sucrose-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 (sucrose synthase, an enzyme) 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, Fig. 5). Quantitative variations are primarily related to the width of the cambial zone and the position of cells. This relationship indirectly supports the hypothesis defining xylem formation as a partially independent system after the external signal from higher levels of regulation has been accepted.

### **3.4 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, biophysical processes connected to between-cell gradients, and properties of membranes and organization of the cell wall (Catesson 1994; Demura and Fukuda 1994; 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 arise from the mechanical properties radial walls need for subsequent radial growth (Roland 1978; Catesson and Roland 1981). 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 nonuniformity 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  $\mu\text{m}$ ). In latewood tracheids, cell wall thickness can reach 7–8  $\mu\text{m}$ . 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. As of now the issue has not been 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 Brown and Sax 1962; Wilson 1964; Zahner 1968; Larson 1969; Denne and Dodd 1981; Creber and Chaloner 1984; Vaganov et al. 1985; Carlquist 1988a, b; Downes and Turvey 1990; Antonova and Stasova 1993; Lev-Yadun and Aloni 1995; Savidge 1996).

In early works conducted by Wodzicki (1971), Skene (1972), and Denne (1971) 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  $\mu\text{m}^2$  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  $\mu\text{m}^2/\text{day}$ , and in trees with a well-developed crown at the beginning of a season, 6–7  $\mu\text{m}^2/\text{day}$  (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  $\mu\text{m}^2/\text{day}$ . Similarly, Sviderskaya (1999) obtained a rate of cell wall deposition of 5–7  $\mu\text{m}^2/\text{day}$  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 through the predetermination of final tracheid radial dimension and cell wall thickness may be mediated through control of the rates of synthesis of different components of the tangential and radial walls.

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 (Fukuda 1996; Graham 1996; Hertzberg et al. 2001; Chaffey et al. 2002; Ito and Fukuda 2002; Goujon et al. 2003; Kirst 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 demonstrated 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 depend 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 (Taiz 1984; Catesson 1990, 1994; 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 process determines the bridge between the first and last stages of tracheid differentiation through the activity of genes involved in the cell cycle and cell wall thickening.

### **3.5 Effect of climatic factors on tree-ring structure (light, temperature, and water)**

#### **3.5.1 Temperature**

Dendrochronologists have made many investigations of the effect of temperature on radial tree growth and wood density (Fritts 1976; Hughes et al. 1982; Schweingruber 1996). Significantly less data are available for the temperature effect on the anatomical features of tree rings. Much of the relevant research was conducted on trees growing at high latitudes where temperature is presumably a leading limiting factor. Some research concerning anatomical structure was made on seedlings in controlled conditions. There are some common findings:

1. Temperature is the most important factor for growth initiation in boreal and temperate climates (Creber and Chaloner 1984; Iqbal 1990). At high latitudes, growth (new cell production) ceases in about the middle of August and the duration of the season of wood production is mainly determined by the starting date of cambial activity (Mikola 1962). Leikola (1969) showed that a 0.5°C deviation in the mean April–May temperature caused significant shifts in the starting date of cambial activity. For the Siberian subarctic, we found early summer (mid-June to mid-July) temperature and snowmelt timing to be very important for the variation in radial growth of larch trees (Hughes et al. 1999; Vaganov et al. 1999; Kirilyanov et al. 2003). Wood production ceases at a much higher temperature than is necessary for its initiation (Denne 1971).

One of the best examples of environmentally controlled tracheid production and differentiating were given in a recent study of Deslauriers et al. (2003). Analyzing the

kinetics of cells in each phase of tree-ring formation (division, expansion, wall thickening) during seasonal growth and development in *Abies balsamea* L. growing in boreal forest, they demonstrated a high degree of variation in the timing of the beginning of the growing season (about one month), the earlywood-latewood transition (around half of a month), and the end of the growing season (about one month). This result is in a good agreement with other high-latitude observations and simulations (Vaganov et al. 1999; Kirilyanov et al. 2003). On the other hand, Deslauriers et al.(2003) estimated a duration of cell expansion in the stage of cell enlargement that gave significantly shorter times (less than one week for earlywood and 5–10 days for latewood) than those recorded in lower latitudes (Wodzicki 1971; Skene 1972; Antonova et al. 1995; Vaganov et al. 2006). These differences could be genetically determined because of the short season for tree-ring growth and maturation of the tracheids. Deslauriers and Morin (2005) found that cell production in the cambium was correlated with the temperature during the same period. Artificially lagging the daily temperature data even by a single day decreased the correlation with cell production substantially, indicating that the cambium reacted quickly to external environmental variability.

2. At high latitudes, tree-ring width variations correlate well with average summer (June–August) temperature, but maximum density shows a significant correlation with temperature for a larger part of the growing season—for example, May–September (Briffa et al. 1990, 1992, D’Arrigo et al. 1992). A longer growing season due to high temperatures will definitely increase the percentage of latewood in tree rings (Larson 1964).

3. Denne (1971), in experiments with Scots pine (*Pinus sylvestris*) seedlings, showed that a temperature increase from 17.5°C to 27.5°C produced only a 10% increase

in tracheid diameter. Contrary to this, we found a significant increase of tracheid diameter in the earlywood of larch tree rings near the northern timberline associated with a long-term summer temperature increase (Vaganov 1996c). Note that these effects of early summer temperature on earlywood tracheid diameter occur in the temperature range 5–14°C. In more southerly sites where the early summer temperatures were higher (between 12°C and 19°C), the effect of temperature on tracheid diameter was diminished because the temperature was no longer in the range where it was clearly limiting (Vaganov 1996c). Under conditions close to optimal temperature (as in Denne's experiments), the limiting effect of temperature on tracheid diameter is probably small.

4. Temperature and tracheid wall thickness were inversely correlated in several conifer species (Wodzicki 1971). Similar data were obtained by Antonova and Stasova (1993, 1997). This result contradicts results from maximum latewood density, which is mainly determined by cell wall thickness. At the upper elevations or northern timberlines, rings with thin-walled cells in the latewood (so-called 'light rings'), are produced by a cold autumn or sharp cooling at the end of summer (Filion et al. 1986; Schweingruber 1993).

Many of the contradictions in publications on the effect of temperature on tracheid dimensions (diameter, wall thickness) are caused by other uncontrolled but important external factors, such as water supply or light intensity, and by uncertainties in the ranges of strong limitation of one factor and alteration of the limit by another factor. For example, Denne (1971) chose a temperature range that is close to optimal for growth. Thus there is no pronounced effect of temperature on anatomical structure. In the case of Antonova and Stasova (1993, 1997), there was no control of the soil water content during the production and formation of latewood tracheids. Hence the apparent negative effect

of temperature could come from its indirect effect on water loss from soil due to increased evapotranspiration.

### **3.5.2 Water**

The availability of soil water may affect the growth rate and formation of wood, both at long timescales and within a season (Zahner and Oliver 1962; Kozlowski 1968; Zahner 1968; Creber and Chaloner 1984; Bräuning 1999). For example, pine in marshy conditions forms not only narrower tree rings, but rings with smaller absolute size and proportion of latewood. In periods of suppressed growth, a tree ring may have only one or two cells of earlywood and one small-sized, thin-walled latewood cell in each file. Considerable variability of cell size and cell wall thickness may occur within wide tree rings grown in favorable conditions. ‘False’ rings may be produced when small, thick-walled cells are seen at the beginning of the latewood zone and are followed by larger, thin-walled cells. The formation of ‘false’ rings is a common phenomenon when intraseasonal droughts occur in a precisely designated rainy season, as seen, for example, in the mountains of the American Southwest. The layer of larger cells is produced in response to the arrival of the rains at the northern fringes of the Mexican monsoon in early July. However, during certain years, the trees can completely stop growth in the ‘pre-summer’ drought period; and in such a case a ‘false’ ring identified on anatomical features does not differ from the annual ring.

### **3.5.3 Light**

Even if we may reasonably assume that temperature and water availability have direct effects on cambial activity, in the case of light the effect is undoubtedly indirect, being mediated through the photosynthetic tissues. The control of growth by light intensity and photoperiod (day length) has been examined in several monographs and textbooks (Alexeev 1975; Howe et al. 1995; Kozłowski and Pallardy 1997). It is not possible here to review much of the work in which the effect of light on the height or diameter growth (and tree-ring width) of trees was studied. We will briefly consider some results concerning the influence of light intensity and photoperiod on the anatomy of conifer tree rings.

Richardson (1964) showed a clear positive effect of light intensity and day length on tracheid cell wall thickness and mean lumen diameter in xylem formed in stems of Sitka spruce (*Picea sitchensis*) seedlings. Larson (1962, 1964) showed an obvious effect of photoperiod on anatomical characteristics of tracheids in xylem formed in *Pinus resinosa* seedlings. He found that, on a long day, the formation of larger tracheids was associated with greater needle length. He showed that this effect was clearly photoperiodic rather than simply photosynthetic. Day length influences wood density by controlling the formation of earlywood and latewood cell types through the types of cambial derivatives, rather than the width of the xylem increment (Waisel and Fahn 1956). The growth and formation of earlywood was resumed if the trees were returned to the long day-length condition (Wareing and Roberts 1956).

### **3.6 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, however, a 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

$$\begin{aligned}\frac{dN}{dt} &= f_1 \{x_i(t_j)\} \\ \frac{dD}{dt} &= f_2 \{x_i(t_j)\} \\ \frac{dCWT}{dt} &= f_3 \{x_i(t_j)\}\end{aligned}\quad (1)$$

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 ( $CWT$ ).

$$TR_{\text{portion}} = f \{f_1[x_i(t_j)], f_2[x_i(t_{j+k})], f_3[x_i(t_{j+m})]\} \quad (2)$$

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 analysis 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 temperatures, when the last forming tracheids enlarge and thicken. 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 1996a). Reflecting this, equation (1) can be rewritten:

$$\begin{aligned}
\frac{dN}{dt} &= f_1\{x_i(t_j)\} \\
\frac{dD}{dt} &= f_2\{f_1\} \\
\frac{dCWT}{dt} &= f_3\{f_1, f_2\}
\end{aligned}
\tag{3}$$

From this, several theoretical and experimental considerations follow:

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 nonrandom 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 result suggests a decreasing influence of climatic variations if one considers the within-ring components, in contrast to interannual rings 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 to test this model by simulation of climatically induced variations of tree-ring width and cell dimension in different climates (from northern timberline to semiarid regions) (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.

### **3.7 Process model description**

The Vaganov-Shashkin 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.

### 3.7.1 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 (Fig. 3.2, inset). Four parameters define the shape of the trapezoidal growth functions—a minimum ( $g(t) = 0$ ), lower and upper optimal bounds ( $g(t) = 1$ ), and a maximum ( $g(t) = 0$ ). Between the 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

$$G(t) = g_E(t) \cdot \min[g_T(t), g_w(t)] \quad (4)$$

Water balance is computed daily by the model as a function of precipitation (as well as snowmelt), evaporation (which is a function of temperature), and runoff

(Thorntwaite and Mather 1955). Solar irradiance is determined by the model from the latitude of the meteorological station from which the input data are 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—that is, it is controlled by the most limiting factor (e.g., Fritts 1976)—at a daily resolution.

A recent study of intra-annual radial growth rates in trees of different species located in different sites and environmental conditions reveals that maximum growth rate of weekly cell production and variations in stem circumference at high-latitude sites occurred around the time of maximum day length (Rossi et al. 2006). These data were obtained by smoothing seasonal growth curves by using the Gompertz equation and transferring the cumulative curves into differential rates of cell division, expansion, and maturation. These data in general are in good agreement with what we assume in equation (4), although equation (4) has more flexibility because of the combination of day length and temperature for determining the maximum growth rate. Observations at high latitudes indicate that the maximum growth rate, as well as the beginning of the growing season, may vary greatly, even as late as the summer solstice (Deslauriers et al. 2003; Vaganov et al. 2006). Use of the Gompertz equation for quantitative description of tree-ring growth is ultimately a statistical tool and not a biological model, but it is potentially useful for combining subannual observations of cambial dynamics and diameter growth with mechanistic modeling at daily to weekly resolutions.

### **3.7.2 Cambial Block**

The Cambial Block uses the output from the Growth Block to determine the rate at which cambial cells grow and divide (Figs. 3.2, 3.3). 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 (Fig. 3.2). 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 that 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.

The Vaganov-Shashkin model 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 CO<sub>2</sub> concentration over the past 150 years. Nor are additional biological or ecological influences on patterns of tree-ring formation modeled, including those 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.

### **3.8 Model applications**

Temporal variability in the relationship between climate and tree-ring-derived proxies has 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 characteristic 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<sub>2</sub> 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 that 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 (Anchukaitis et al. 2006; Evans et al. 2006), which make direct comparisons impossible. We stress that implicit in our interpretation of the model results presented here is the following assumption: If we can establish that the simulations are consistent with the corresponding observed chronologies, the VS model includes the most critical processes linking climate to annual tree-ring formation.

### **3.8.1 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 (Fig. 3.4), and using the same set of fixed parameters and closely collocated meteorological station data. Despite neglecting adjustment of model parameters to fit local site characteristics, seven of eight simulations are significantly correlated with actual chronologies at or above the 95% confidence level. Four of eight correlations between 5-year means of the simulations and actual chronologies were significant at or above the 90% confidence level. Cook and Pederson (chapter 4, 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, New York, 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).

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 ( $p < 0.05$ ); Fig. 3.5c). The significance of  $r$  was not highly sensitive to the exact value of the soil moisture drainage parameter we chose. Correlation functions for simulated and actual chronologies are similar (Fig. 3.5a, b). 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 (chapter 4, 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 (Fig. 3.5d). The modeling results suggest that early season growth is strongly

tioned 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 (the complex and potentially unexpected interaction of biotic and abiotic elements) from statistics (uncertainty arising from random noise).

### **3.8.2 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 (Fig. 3.6). 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 by 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.

### **3.8.3 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 500 km 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 (PDSI) 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 (Fig. 3.7). 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 such non-climatic biases from candidate proxy dendroclimatic datasets are under way.

#### **3.8.4 Uncertainties and caveats**

There are several important caveats that should accompany the interpretation of existing simulation experiments as well as the future applications of the VS model to new research questions in dendroclimatology. One of the strengths of the model is that it operates on a daily timescale, and is therefore capable of accurately simulating the response of trees to rapidly changing seasonal climate conditions (e.g. Deslauriers and Morin 2005). The daily data requirements of the model, however, restrict both its temporal and spatial application, due the limited length and general unavailability of meteorological observations of the appropriate timescale, particularly from the remote alpine or tree line regions of particular interest to dendroclimatologists. Even where daily meteorological data can be found, stations may be located at considerable distance from the tree-ring chronology site, almost always at a lower elevation, and often with different exposure and topography. While differences in temperature between site and station can usually be evaluated and reasonably corrected, it is quite difficult to do so for

precipitation. The length of the daily meteorological records also limits the period over which model skill can be evaluated against the available tree-ring chronologies. At the same time, many tree-ring chronologies in many parts of the world were originally collected in the 1970s and 1980s and have not yet been updated, further limiting the overlap between simulated and actual tree-ring data.

Additional uncertainties derive from model parameter specification. The model has 31 adjustable parameters (Vaganov et al. 2006), many of which were originally developed from empirical research on cold (Siberia) or dry (Arizona) environments, but which are potentially poorly constrained in other regions. With our collaborators, we are currently developing and testing two complementary approaches to evaluating and reducing uncertainties associated with parameter choices. Ongoing studies in Siberia are focused on improving the empirical basis for model parameterization across a range of environments and site conditions. Another approach is to use Monte Carlo bootstrapping techniques to develop probabilistic estimates of the sensitivity of simulation results to parameter choices, and to identify those that are most important. An additional complication is the potential for species-specific parameters. Although we have successfully applied the model with the default ('Siberian') parameters to a range of species (Evans et al. 2006), there are indications that the model performs better for some species than for others. We are currently investigating the extent to which this differential skill is a consequence of site environment or species characteristics.

As was discussed in the previous section, our specific research questions as well as data requirements have led us to use a variety of approaches in simulating tree-ring width chronologies. Evaluations of the model skill as compared with observations have therefore employed a range of statistical techniques, including correlation, principal

components (Anchukaitis et al. 2006), and spatiotemporal analysis of large overlapping networks (Evans et al. 2006). Each of these approaches necessarily has its own underlying assumptions and potential biases, which must be kept in mind in testing the model against existing tree-ring data.

### **3.9 Conclusion**

The biological, chemical, and physical processes that link the external environment to the characteristics of annual growth rings in trees form the necessary basis for dendroclimatological research. Although ultimately the incremental basal diameter growth of trees cannot proceed without biochemical pathways, structures, and substrates associated with both the crown and the roots, the fundamental processes that give rise to basal growth and the characteristics and anatomical features of the annual ring are those associated with cellular growth and division in the cambium. Here, we have demonstrated that understanding and modeling the environmental controls on tree-ring formation as arising in part from direct climatic influences on the dynamic cambium allow us to reproduce the observed phenomenology of intra-annual patterns of tree growth as well as the annual and interannual patterns of ring width variability as observed in a variety of species and sites, and across different spatial scales. However, much future work is necessary at the intersection of dendrochronology, tree physiology, and biochemistry in order to better describe and understand the relationships between photosynthesis, carbon assimilation and storage, and tree-ring width, as well as the cellular processes or structures that might account for and permit the direct environmental influences on dividing and growing cells in the cambium.

By linking the external environmental controls on the formation of tree-ring proxies to processes that primarily influence the cambial zone, the VS model allows us to produce synthetic tree-ring series that 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 that 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 United States 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 non-climatic 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 3.1. Seasonal dynamics of radial tracheid size (filled triangles), cell number in cambial zone (dashed line, divide by 5), and specific growth rate (solid line) in (a) *Abies sibirica* and (b) *Pinus sylvestris* (from 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 at that time. 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 3.2. 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 nondifferentiated cell reaches a critical size, it enters and completes the mitotic cycle, continuing its subsequent growth at a constant, environmentally independent growth rate until division occurs, resulting in two cells, each half the size of the original mother cell. Once differentiated, cells can no longer divide and go on to complete the subsequent stages of expansion and cell wall thickening.

Figure 3.3. Schematic diagram showing the functions that 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,  $V_{\text{cr}}$ , defines the division rate at which cells still in the cambium enter dormancy.

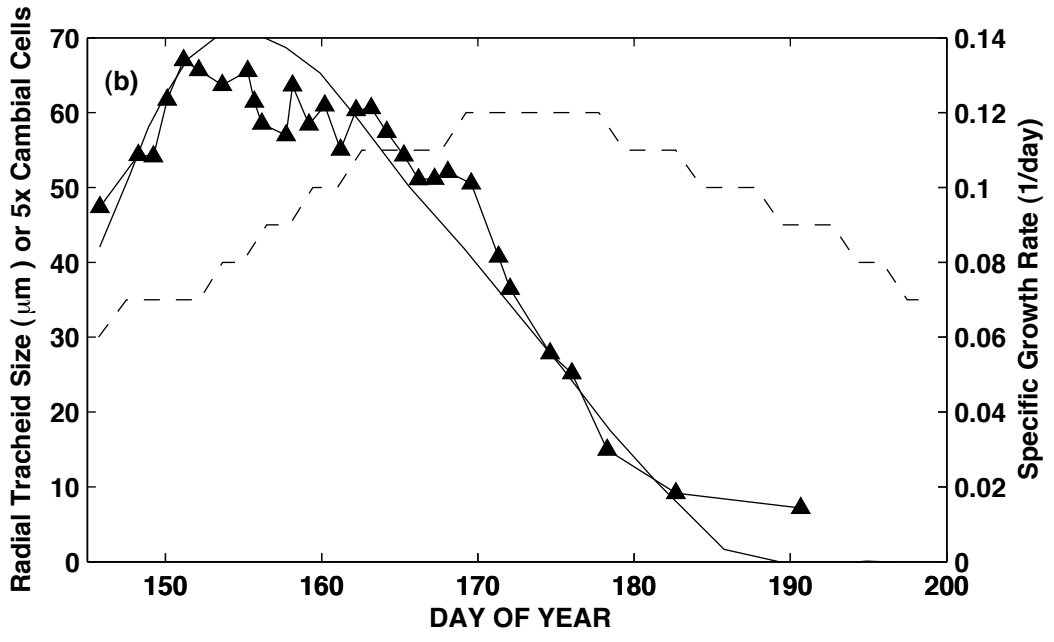
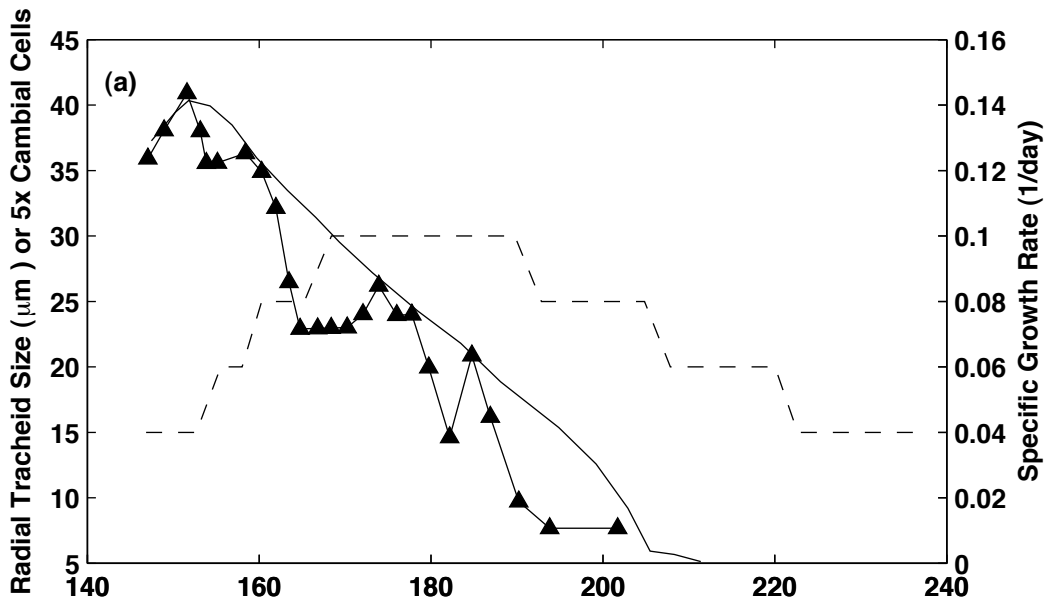
Figure 3.4. Time series of Vaganov-Shashkin model simulations (dashed lines) compared with actual ring width chronologies (solid lines) from high-latitude sites across Russia. Correlations are for annual and five year averages. \*, \*\*, \*\*\* indicate one-tailed significance at  $p < 0.1$ , 0.05, 0.01 levels, respectively, considering effective degrees of freedom given series lag-1 autocorrelations. (a) Chokurdakh (Coku) (147.9°E, 70.6°N). (b) Hatanga (102.5°E, 72°N). (c) Olenek (112.4°E, 68.5°N). (d) Tura (100.0°E, 64.2°N). (e) Turuchan (88.0°E, 65.8°N). (f) Ulan-Ude (107.4°E, 51.8°N). (g) Verhoyn (133.4°E, 67.6°N). (h) Zigansk (123.4°E, 66.8°N). Results from Evans et al. (2006).

Figure 3.5. 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.

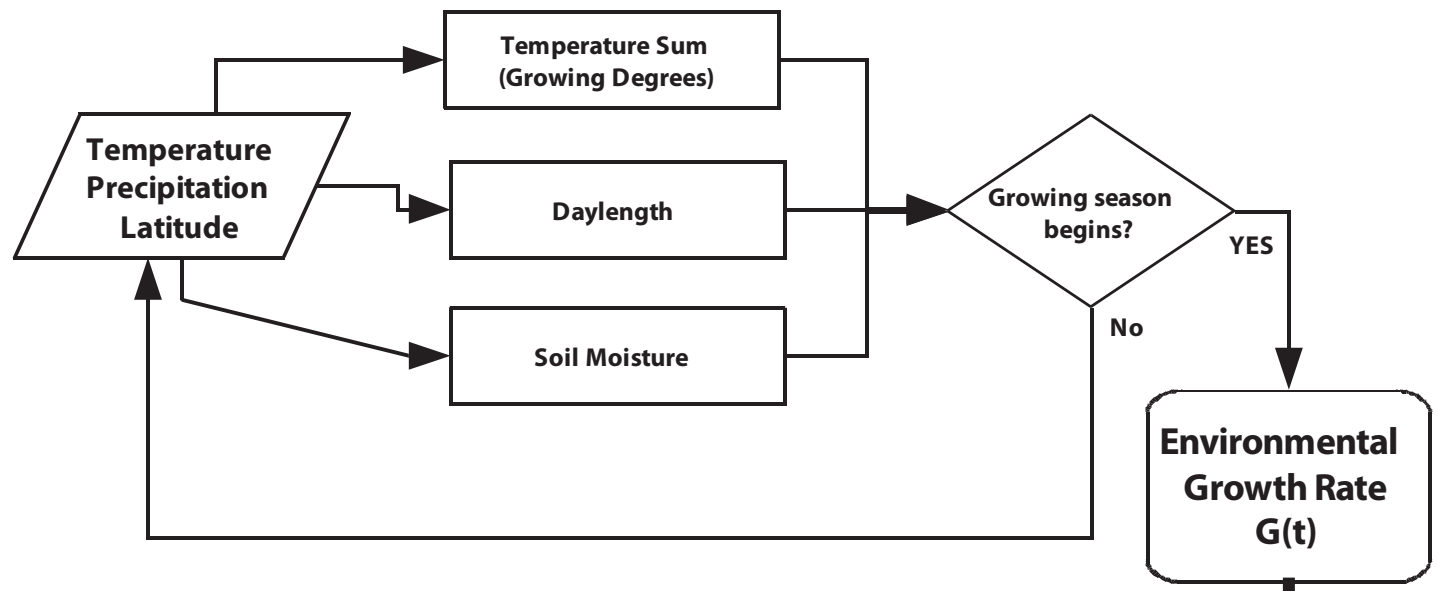
Dashed lines of the same color show the 95% two-tailed confidence intervals from bootstrapping (1,000 draws with replacement; Biondi and Waikul [2004]). Values above these lines can be considered statistically significant, accounting for the number of independent predictors (c) The simulation (black 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, section 3.8.1, for discussion.

Figure 3.6. 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 (March–April–May, 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 3.6b; three-letter identifiers denote 10 ring width chronology sites in Figure 3.6c. Reprinted with permission from Anchukaitis et al. (2006).

Figure 3.7. Significance of annual correlations of simulated and actual tree-ring width data for 8 sites across Russia (Fig. 3.4) and 190 sites in North America from the Mann et al. (1998) dataset. Black and gray 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).



**Growth (Environmental) Block [Daily Time Step]**      $G(t) = g_E(t) \cdot \min [g_T(t), g_W(t)]$



**Cambial Block, for each cell in annual file**      $f\{j, G(t)\}$

