

1 Introduction and Factors Influencing the Seasonal Growth of Trees

1.1 Introduction

1.1.1 Perspective

Our aim in this book is to introduce the way of thinking about the environmental control of tree-ring variability in conifers that is expressed clearly in its title: “*Growth dynamics of conifer tree rings: images of past and future environments*”. In particular, each ring contains an image of the time when the ring formed, projected onto the ring’s size, structure and composition. The lens through which this projection occurs is the vascular cambium, the site of development of each year’s ring. We focus on its dynamics. Our particular perspective comes from our chosen task – the extraction of an image of past environments, especially climate variability, from the incomparable natural archives that tree rings offer. The emphasis on variability leads naturally to a dynamic rather than a static view of climate/tree-ring interactions.

In order to best use our understanding of the environmental control of tree-ring variability, simulation models have been developed. The aim is to capture those features of the system under investigation that are essential for the description of the behavior of interest, no more and no less. Our specific objective is to simulate the interannual and decadal variability of conifer tree rings as it is driven by climate variability. We do this by focusing strongly, and uniquely, on the direct environmental control of cambial activity, without any explicit treatment of photosynthesis, respiration, and transpiration. This may seem a radical, perhaps even extreme, approach to the readers of this series, who are especially aware of the complexities of ecological systems and the many physical, biophysical, and biological processes that may be linked to any particular phenomenon in myriad modalities. We hope to convince the reader that, even so, this strategy has merit.

Process-based simulation modeling should be viewed as an addition to the dendroclimatologists’ already versatile toolkit. The mainly inductive empiri-

cal–statistical approach used in this field has helped change the way we think about environmental variability on multi-year timescales and large spatial scales, up to global. It can be complemented and enhanced by the application of understanding derived from experimental–deductive work more focused on daily to seasonal timescales at cellular and even biochemical levels. We recognize that we risk double jeopardy, both for trying to combine these ways of studying nature, and for perceived inadequacies from the point of view of either group of specialists. This will be a price worth paying, if those focused only on the history of large-scale climate variability gain some appreciation for the nature of the natural archive they depend on and its meaning for their interpretations, and those focused on the precise mechanisms of environmental control of xylogenesis are introduced to the many phenomena at larger scales that dendroclimatology reveals.

1.1.2 The Structure of This Book

The main factors affecting the seasonal growth of trees are introduced in this chapter. In Chap. 2, the reader is introduced to the idea of the tree ring’s size and internal structure as an image of the growth conditions that existed at the time it was formed. The processes of ring development are set in a kinetic, seasonal context in Chaps 3, 4, and 5, which deal with the production, expansion, and maturation of xylem cells, respectively. A conceptual scheme for the environmental control of xylem differentiation is described in Chap. 6. This leads, in Chap. 7, to a discussion of modeling of external influence on tree-ring structure and, in particular to a description of the Vaganov–Shashkin (VS) model. The VS model is characterized by a strong emphasis on cambial activity, as if directly influenced by the external environment. Examples of the application of the VS model designed to illustrate its potential in tackling some pressing scientific questions are given in Chap. 8. An expansion of this modeling approach designed to explicitly include the influence of the canopy and the forest stand is described in Chap. 9. The Epilogue (Chap. 10) contains some parting thoughts.

1.2 The Environment and Tree-Ring Formation

The formation of annual rings in woody plants, as well as the formation of annual and growth layers in “recording structures” of other organisms (Mina and Klevezal 1970), is an outcome of the seasonal periodicity of growth processes. The growth of a woody plant represents an increase in the weight and volume of the whole plant or its parts as the result of the formation of new cells and the increase in their size (Reimers 1991). The seasonal periodicity or

rhythm of biological processes in a woody plant is determined by regular environmental fluctuations associated with the annual cycle. The expression of these seasonal rhythms depends on the species of woody plant and the local conditions where the plant is growing.

Zones of formation of new cells in plants are called meristems. Apical meristems (meristems of shoots and roots) provide growth in height and length of the underground parts. Tree stems and roots increase in thickness as the result of the production of wood and bark cells by lateral meristems. There is a genetic relationship between apical and lateral meristems because the lateral meristem or cambium is a product of the apical meristem and consists of cells retaining the potential to proliferate (Zimmermann and Brown 1971). There is also a functional relationship, as demonstrated by the coordination of the processes of growth of different parts of a woody plant in the seasonal rhythm (Sinnot 1963; Kramer and Kozłowski 1983; Kozłowski and Pallardy 1997). Growth hormones are the mediators of this coordination. Their balance, together with assimilates and other nutritious substances, is important for the dynamics of growth processes and the formation of the cell structures of the tissues and organs of the plant (Kozłowski 1968; Philipson et al. 1971; Savidge 1996).

1.3 Internal Factors

We will limit our discussion to those internal factors whose influence on the dynamics of seasonal growth in woody plants has been established convincingly by experiment and observation. The genetic nature of the plant is one of the major factors. Investigating seasonal growth of 18 tree species during one growing season in Denmark, Ladefoged (1952) noted precise differences in phenology, the timing of bud opening, and the initiation of meristem activities in the shoots, stems and roots between different species (Fig. 1.1). He found a difference of three weeks in the date of initiation of new wood cell production amongst the conifer species he observed. The first divisions of lateral meristem cells in spruce (*Picea sitchensis*) stems are observed in the third ten-day period of April, in stems of a Scots pine (*Pinus sylvestris*) right at the beginning of May, and in stems of European larch (*Larix decidua*) only in the middle of May. The data by Henhappl (1965), who studied seasonal growth of seven species of conifers and 11 deciduous species near Freiburg, Germany, during three years, show that initiation of cell division in conifers ranged over 40 days. The earliest was Scots pine (*P. sylvestris*), the latest white pine (*P. strobus*). The length of the growth season varied from 104 days in European larch (*L. decidua*) to 137 days in fir (*Abies alba*).

Cambial initiation begins below the expanding/enlongating buds and the wave of activation propagates basipetally, so that the cambium at the base of

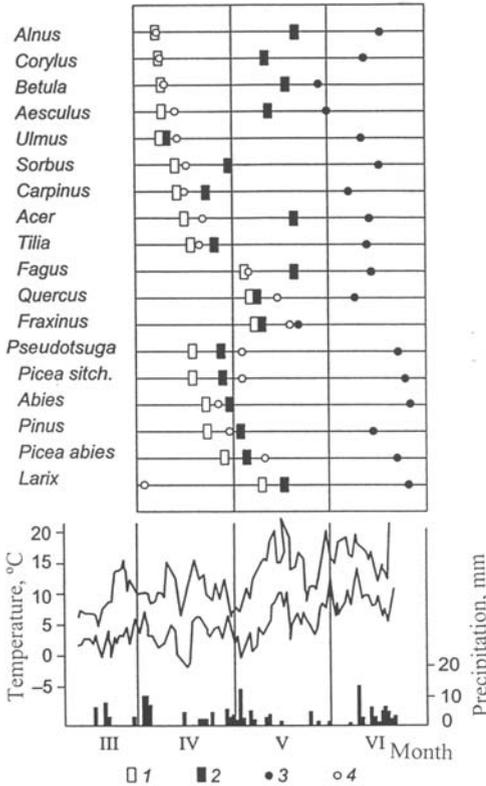
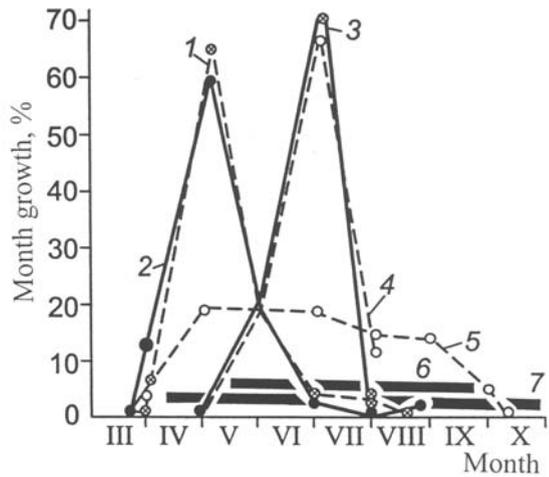


Fig. 1.1. Timing of onset of cambial activity in conifers and angiosperms in relationship to temperature and precipitation in Denmark. 1 At the bud base, 2 at breast height, 3 roots 10 cm deep and 1.5 m from the stem, 4 bud opening. Notice the time-lag between cambial activity in the branch and the root. This is possibly due to regulation through growth hormones (Ladefoged 1952)

the tree is the last to divide and differentiate (Zimmermann and Brown 1971; Kramer and Kozłowski 1983; Kozłowski and Pallardy 1997). Then, in the fall, the reverse process begins when the oldest cambial tissues (at the base of the tree) become dormant first and the process propagates acropetally back to the base of the apical meristems of the crown.

Differences between species are found not only in the timing of the initiation and termination of cell divisions in meristems, but also in the seasonal dynamics of growth. Ladefoged (1952) divided tree species into three groups on the basis of qualitative analysis of growth-rate curves: (1) with a growth rate maximum in the first third of the season, (2) with a more symmetrical curve of growth rate, (3) with uniform growth rate during the growing season. Similarly, in the Moscow region, Scots pine (*P. sylvestris*), European fir (*A. alba*), and European larch (*L. decidua*) demonstrate a distinct growth maximum in the first half of the season, while birch (*Betula pendula*) shows a uniform distribution of growth rate throughout the season (Smirnov 1964; Vaganov et al. 1975). The distribution through the season of the rate of growth is related to the characteristics of the species. For example, analysis of the sea-

Fig. 1.2. Types of variation of height growth during the vegetation period in the northern and southern pine ecotypes. Two northern pines have preformed shoots and one shoot-forming period in a year. The southern pines have periodic shoot growth. 1 *Pinus strobus* L. (North Carolina), 2 *P. resinosa* Ait. (North Carolina), 3 *P. resinosa* Ait. (New Hampshire), 4 *P. strobus* L. (New Hampshire), 5 average for all southern pines, 6, 7 frost-free period in New Hampshire and North Carolina, accordingly (Kramer and Kozlowski 1983)



sonal dynamics of growth of different species of pines (*P. strobus* and *P. resinosa*) in the forests of the south- and northeastern United States reveals that northern ecotypes have an “explosive” character of seasonal growth rate change, whereas southern ecotypes have a more uniform distribution of growth rate during the season (Fig. 1.2; Kramer and Kozlowski 1983). This difference exists because the northern ecotypes have preformed shoots (limited growth) and only one period of shoot formation per year, whereas continuing periodic growth occurs in the southern ecotypes. Spurr and Barnes (1980) report differences in seasonal dynamics of growth rate (“explosive” or uniform) between *P. rigida*, *P. densiflora*, and *P. banksiana*.

The seasonal growth of shoots and needles (foliage), through the hormonal control of cambial activity, is of central importance to the character and distribution of the seasonal growth rate of stem wood (see reviews in Kramer and Kozlowski 1983; Zimmermann 1964; Zimmermann and Brown 1971; Barnett 1981; Savidge 1996). It is through this means that the processes of development of various tissues and organs are coordinated within the annual cycle, in a manner that varies from species to species. This is illustrated vividly by species-specific patterns of coordination of growth of above-ground (shoots) and underground (roots) parts of woody plants (Fig. 1.3; Lyr et al. 1974). Not only do the maximum increments vary between species, but so do the beginning, ending, and duration of the linear growth of shoots and roots. The coordination of the seasonal dynamics of growth of the various parts of woody plants results in allometric relations between them during the growth and development of the woody plant and the stand (Utkin 1982; Terskov and Vaganov 1978; Vaganov 1981; Utkin et al. 1996).



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